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SELECTION INDICES FOR THE IMPROVEMENT OF OPAQUE-2 MAIZE

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Selection indices for the improvement of opaque-2 maize

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INTRODUCTION

Maize is a productive cereal crop, important in human diets and animal rations. Maize grain, however, is of poor nutritional quality because of poor amino acid balance in the protein fraction. Zein, the major component of maize endosperm protein, is deficient in the essential amino acids lysine and tryptophan.

The opaque-2 recessive gene has been shown to increase the quality of maize endosperm protein by acting as a partial suppressor of zein synthesis. However, the potential use of opaque-2 maize as a source of food and feed has not been realized, because of poor agronomic performance, chiefly low yield and soft kernels susceptible to damage by ear-rotting fungi and harvesting equipment. Studies of heritability and relationships among traits in opaque-2 populations have shown that many important traits are correlated in an unfavorable manner, so that direct selection to improve one character would be expected to cause undesirable changes in another. However, substantial genetic variation for agronomic, protein, and kernel quality traits exists. Moreover, the deleterious agronomic effects of the opaque-2 gene vary in degree depending on genetic background. Thus, a recurrent selection approach to the improvement of opaque-2 populations has frequently been proposed.

Selection indices have long been considered an effective means of effecting genetic improvement when more than one character must be considered. Theoretical as well as applied research has attributed unique advantages to the selection index approach. Application of selection indices by plant breeders, however, has been somewhat limited for several reasons. The problem of specifying selection goals for the different traits is unavoidable and presents many subtleties. Warnings have often been given concerning the effects of using estimates of population variances and covariances in place of the unknown "true" parameter values. The suggestion has been made that different types of indices might differ with respect to reliability of prediction of genetic advance. Nevertheless, these complicating factors apply to the general problem of multi-trait selection and do not necessarily weigh more heavily against the selection index than against other approaches to that problem. The potential benefits of selection indices will be greatest where attention to more than one character is indispensable, as it is with opaque-2 maize.

The principal objective of this study was to calculate and compare selection indices for the improvement of opaque-2 maize, taking into account to the extent practicable the reliability of predicted response of an index as well as its

expected genetic advance. Secondary objectives were to determine the importance of various agronomic, protein, and kernel quality traits to the breeder of opaque-2 maize, to compare three recurrent selection schemes with respect to the progress possible through index selection, and to compare the usefulness of single plant and replicated progeny measurements of certain characters.

LITERATURE REVIEW

Index Selection

Theory of index selection

The selection index was first proposed by Smith (1936) as a means of taking more than one trait into account when making selections in plant breeding. The index is a weighted sum of the phenotypic values of the traits and is used as the selection criterion. In order to calculate the weights it is necessary to know: 1) the "economic value" associated with each trait, 2) the genotypic and phenotypic variance of each trait, and 3) the genotypic and phenotypic covariances of each pair of traits. Hazel (1943) clarified the genetic theory underlying the index approach and made possible the use of index selection in situations where selection focuses on breeding value, the portion of genetic superiority transmitted to progeny. He also outlined methods for estimating the required variances and covariances, and discussed the incorporation of information from relatives into the index. Methods for obtaining variances and covariances applicable to cross-fertilizing species were illustrated by Robinson et al. (1951) and Mode and Robinson (1959). Subsequent theoretical work has been directed at comparing index selection with other breeding methods, extending the index to a broader range of applications, and modifying the procedure

to better suit breeders' goals and resources. Lin (1978) has reviewed much of this work.

Hazel and Lush (1942) compared index selection with tandem selection and selection by means of independent culling levels for each trait. They showed that, when traits were independent, index selection was the most effective. The more general case of possibly correlated traits was considered by Young (1961), who determined that index selection was in all instances at least as effective as independent culling, which in turn was at least as effective as tandem selection. The superiority of the index approach increased as the number of traits increased, but decreased with increasing difference in economic weights of the traits. Finney (1962) gave a more generalized treatment of Young's (1961) results. According to Young and Weiler (1960), however, index selection may be more costly than the other methods, and the advantage of the index in effectiveness may not be great enough to justify its use in some instances.

Modifications of selection index theory have been made to meet particular needs. Legates and Lush (1954) used empirically determined covariances among relatives to construct a selection index for fat production in dairy cattle that incorporated data from a cow and its dam, daughters, and half-sibs. Hanson and Johnson (1956)

developed a method for using data from more than one population to develop an "average" index; i.e., one that would maximize the average genetic advance of the populations. Griffing (1969) presented a solution to the problem of selection in the presence of interaction among genotypes within heterogeneous groups. Van Vleck (1970) considered the case of traits having maternal genetic components. For situations in which information becomes available on different traits at different times, Cochran (1951) suggested a multi-stage selection process and gave a solution for the case where index weights were derived from regression of genotypic value on phenotypic components. Young (1964) discussed the problem further, and Cunningham (1975) gave a general solution together with an algorithm for the incorporation of an index into an index and for adjusting in later stages for the effects of selection in earlier stages.

In many prospective applications of selection indices it is impossible to determine economic values for all traits. Pešek and Baker (1969b) proposed to overcome this problem by substituting specification of the relative gains desired in the traits for economic values.[1] The resulting "desired gain" index yields gains in proportion to those

[1]As Lin (1978) points out, this problem is a special case of the restricted index of Tallis (1962).

specified. Yamada et al. (1975) gave a somewhat more general solution. A solution which would permit assignment of economic values to some traits and desired gains to others was given by Tai (1977).

Various types of restricted indices have been proposed. Restricted indices maximize gain in economic value subject to restrictions on gains in specific traits. Morley (1955) and Kempthorne and Nordskog (1959) considered the restriction that gain in some traits or linear combinations of traits be zero. Tallis (1962) extended this to the case where certain traits are to respond by a fixed amount, while the gains in others are maximized. The approach of Rao (1962) was to restrict the gain in some traits to non-negative values. Cunningham et al. (1970) gave a simple solution incorporating any of these types of restrictions. The restricted index of James (1968) incorporated restrictions on both the gain and the coefficients of the index.

In the initial and most of the subsequent development of the methodology of index selection, it has been assumed that the necessary parameters--genetic and phenotypic variances and covariances--were known without error. In fact, however, these parameters are never known and must be estimated. The effects of errors of parameter estimation on a selection index have been investigated. Williams (1962) believed that such errors could have a substantial effect on

effectiveness of the index. To reduce the magnitude of the problem he suggested that traits that contribute little to the variance of the index and that have small weights could be eliminated. He also suggested that the variance of the expected gain associated with an index be calculated and used to choose the best index. He defined a base index as one in which economic values were used directly as the weights of the index. The use of the base index, which had been earlier suggested by Brim et al. (1959), would, if the difference in predicted gains between the standard Smith (1936) index and the base index were small, reduce the risk brought about by the dependence of the former on parameter estimates.

Harris (1964) used approximate equations and a simulated sampling study to evaluate selection indices that involved parameter estimates. He concluded that the predicted progress from index selection was likely to be biased upward. For an index with two traits in which economic weights were equal, estimation of progress from the index was improved by large genetic variances, positive genetic covariances, negative environmental covariances, or large populations for estimating parameters. Harris agreed with Williams (1962) that a base index would be advantageous in many cases.

Using calculations similar to those of Harris (1964), Sales and Hill (1976b) investigated the effects of sampling

errors on indices designed to improve one trait using the trait itself and correlated traits. They concluded that the extra response expected from including correlated traits would usually be over-predicted. They further stated that the gains achieved might be far from optimal if the parameter estimates were wrong. Sales and Hill (1976a) reported the opposite conclusion when they considered the use of an index of individual along with half-sib and full-sib family records in selection: responses achieved would be near the optimum even if sample estimates of parameters were far from the true values.

A set of parameter estimates may contain inconsistencies, such as correlation estimates greater than 1 in absolute value, or heritabilities greater than 1 or less than 0. Heidhues (1961) and Harris (1964) recommended replacing such estimates by their nearest limits before calculating an index. Hill and Thompson (1978) referred to more subtle inconsistencies, such as a negative estimate of the genetic variance of a linear combination of traits, which would result in a nonpositive definite genetic variance-covariance matrix (Hohn, 1973, p. 375f). They questioned the validity of an index calculated from such a matrix. Under extreme conditions, the use of such an index could result in a net loss in economic value of a population. The probability of

obtaining a nonpositive definite matrix was found to increase with the number of traits in the matrix.

Because of the risks associated with parameter-dependent indices and the costs incurred in estimating the parameters, several investigators have proposed parameter-free or "weight-free" indices. The base index (Brim et al., 1959; Williams, 1962) has already been mentioned. Others include the multiplicative index (Elston, 1963), the realized index (Widstrom, 1974), the phenotypic index (Narain and Mishra, 1975), the rank summation index (Mulamba and Mock, 1978), and the base-standard deviation index.[1]

Application of index selection

Selection indices may be constructed with the goal of using information on more than one trait to control genetic change in one trait or in several traits. When a single trait is to be improved the index is used in order to utilize correlated characters to improve the effectiveness of selection. Many researchers have calculated indices for increasing yield using yield components and other correlated traits (Smith, 1936; Simlote, 1947; Robinson et al., 1951; Abraham et al., 1954; Johnson et al., 1955; Miller et al., 1958; Sikka and Jain, 1958; Shankar et al., 1963; Singh and

[1]Crosbie, T. H., J. J. Mock and O. S. Smith. Comparison of gain predicted by several selection methods for cold tolerance traits of two maize populations. Department of Agronomy, Iowa State University. Submitted for publication.

Mehndiratta, 1970; Thurling, 1974; Singh and Singh, 1976; Yousaf, 1976). Such calculations are useful in identifying the important correlated traits. In some instances direct selection for yield has been predicted to be less effective than a selection index composed solely of yield components (Robinson et al., 1951; Johnson et al., 1955; Singh and Mehndiratta, 1970).

Indices for single-trait improvement have been tested in field studies and results have been mixed. Manning (1956) used yield components to select for lint yield in cotton (Gossypium hirsutum L.). Selections were made for seven generations using an index that was calculated each generation from the most recent data. Total genetic advance was 35%. Caldwell and Weber (1965) applied direct selection and several types of index selection to four populations of soybean (Glycine max L. Merr.) with the objective of improving grain yield. Specific indices (i.e., those with index weights calculated from the parameters of the population to which they were applied) produced only slightly more gain than direct selection. General indices (derived using parameter estimates from a separate experiment with eight populations) and average indices (derived by pooling parameter estimates from the four populations of the index experiment) were slightly less effective than direct selection. Pritchard et al. (1973) reported selection

indices to be inefficient relative to direct selection as a means of improving soybean yields. They cited the cost of data collection required for the index and the large genotype x environment interaction they encountered as reasons for the failure of the index. Radwan and Momtaz (1975) applied indices to individual F_2 plants and F_2-derived lines of flax (Linum usitatissium L.). An index that included grain yield, straw yield, and maturity was superior to indices involving only two of the three characters and to direct selection for improving grain yield.

The theoretical advantage of selection indices over other methods of multi-trait selection (Hazel and Lush, 1942; Young, 1961) has been examined in simulation and in experiments with living material. Pešek and Baker (1969a) conducted a simulation of index and tandem selection in a self-fertilizing species. They assumed that each of two traits was controlled by five loci, with repulsion linkages responsible for a negative correlation. Different linkage intensities, levels of environmental variability, and sets of economic weights were used, and, in all instances, two generations of index selection produced a greater response than one generation of selection on each trait individually. Elgin et al. (1970) used tandem selection, independent culling, a Smith (1936) index, and a base index during five cycles to improve five traits in alfalfa (Medicago sativa L.). The

two indices were similar in effectiveness, with independent culling third, and tandem selection (i.e., selection for a different trait in each cycle) least effective. Eagles and Frey (1974) compared selection methods for improving economic value (grain and straw yield) of oat (Avena sativa L.) lines. The base index and the Smith (1936) index did not differ appreciably in actual or predicted gain, while independent culling produced somewhat smaller gains than the indices. Rasmuson (1964) found independent culling superior to index selection when both were applied to increase sternopleural and abdominal bristle number in Drosophila melanogaster. When selection was for low bristle number, however, the index was the more effective. Tandem selection was inferior to the other methods under both high and low selection. Sen and Robertson (1964) found independent culling more effective than an index in one experiment, but the reverse in a second experiment.

Rosielle and Frey (1975) considered a restricted selection index for improving grain yield of oats without producing undesirable genetic changes in height and maturity. The restricted index was expected to give 57% as much gain for yield as the unrestricted index. In the application of a similar restricted index, Rosielle et al. (1977) obtained good agreement between predicted and actual responses in economic and restricted traits. Predicted advances in

economic value were overestimated with unrestricted indices.

Kauffman and Dudley (1979) used a desired gain index with half-sib family testing and mass selection to improve grain yield and protein content of maize (Zea mays L.). Despite a negative correlation between the traits, simultaneous improvement in both was achieved. A second desired gain index designed to increase protein content without changing kernel weight was also successful.

Saad El-Din (1979) compared several selection indices for improving grain yield and economic value (grain and straw yield) of oat lines. Indices incorporating grain yield and one secondary trait produced up to 20% more actual gain in yield than did direct selection for yield. No index, however, improved economic weight more than direct selection for yield.

Brim et al. (1959) compared indices that included up to six traits for improving economic value in two populations of soybean. Economic value was determined by the production of oil and protein, and three ratios of oil price to protein price were considered. The relative ranking of indices by expected gain was sensitive to changes in price ratio in one population, but not in the other. In both populations and at all price ratios, an index of two simply-inherited traits, seed weight and fruiting period, was expected to produce gains nearly as high as or higher

than those from direct selection for yield of grain, protein, or oil.

Caldwell et al. (1966), in a comparison of seven selection indices for soybean, concluded that the set of weights needed for maximum advance in yield of protein or oil was very similar to that needed to maximize grain yield. No index produced an actual gain in yield significantly exceeding the gain from direct selection.

Subandi et al. (1973) compared a multiplicative index (Elston, 1963) with Smith (1936) indices. Their objective was to improve machine-harvestable yield in maize, and the traits considered were yield (hand-harvested), stalk lodging, and the percentage of dropped ears. The multiplicative index [I = yield x (100 - % stalk lodging) x (100 - % dropped ears)] and a Smith index produced expected gains in machine-harvestable yield of 42% and 44%, respectively, above what would have been achieved through direct selection for hand-harvested yield. The multiplicative index was recommended for situations where economic value could be defined in this manner.

Singh and Bellman (1974) used simulation to compare a multiplicative index of two traits with two Smith (1936) indices, one based on estimates of additive genetic parameters, the other on broad-sense estimates of genetic parameters. Two levels of linkage were considered. The

Smith indices were superior to the multiplicative index in gain, but the multiplicative index was less sensitive to changes in linkage level. Tighter linkage lowered the effectiveness of all indices.

Pešek and Baker (1970) used a desired gain index to improve four characters of wheat (Triticum aestivum L.). Expected and observed gains were dissimilar, perhaps because of a small test population. Gain for yield was much higher than expected, while gains in the other traits were lower.

Matzinger et al. (1976) reported on five cycles of mass selection in tobacco (Nicotiana tabacum L.), in which an index was used to increase leaf number while decreasing plant height. Leaf number and plant height had a high positive correlation (r = 0.67). The index was recalculated in each cycle using the most recent estimate of phenotypic variances and covariances. Genetic variances and covariances were assumed to be constant over cycles. The index was successful in producing shorter plants with more leaves; compared to direct selection carried out separately for leaf number and plant height, the index produced 42% and 31% as much gain in the respective traits.

Crosbie et al.[1] compared several types of selection

[1]Crosbie, T. H., J. J. Mock and O. S. Smith. Comparison of gain predicted by several selection methods for cold tolerance traits of two maize populations. Department of Agronomy, Iowa State University. Submitted for publication.

indices for improving three cold tolerance traits in maize. Applied to data from two populations, the rank-summation index, the multiplicative index, and a base-standard deviation index, in which the reciprocal of the phenotypic standard deviation of each trait was used as its weight, ranked the families very similarly. These indices were favored over Smith (1936) and desired gain indices because they combined satisfactory predicted gains with simplicity of use.

Andrus and Bohn (1967) applied a base index of sixteen fruit characters to the improvement of cantaloup (Cucumis melo L.). Most characters were improved during nine cycles of mass selection (without recombination). There was no loss of variability due to selection.

Suwantaradon et al. (1975) compared three types of indices (Smith (1936), base, and desired gain) in the application of two recurrent selection schemes (S_1 testing and S_2 testing with evaluation of some traits in the S_1) to maize. Relative economic weights and desired gains were assigned arbitrarily to the seven traits used in the indices. The desired gain indices produced only 54% as much expected aggregate genetic advance as the Smith index, a result which may be attributable to the particular set of economic weights and desired gains they used. The base index was expected to produce 96% as much gain as the Smith index. Of the recurrent

selection schemes, S_1 testing was preferred because of expected gain and cost.

Correlated response and predicted vs. actual gain

Selection indices have frequently been considered and occasionally applied by plant breeders. Most reports favor the use of indices when it is desired to control genetic change in more than one trait. Index selection is more dependent than direct selection upon the reliability of predictions of gain, particularly upon predictions of correlated response. The reason for this is that a selection index, unless it corresponds exactly to economic value, is a trait used only to produce advance in other traits. Genetic values of individual traits change depending upon their correlations with the index. Consequently, the question of the accuracy of predicted gains for direct and indirect selection is important.

Table 1 summarizes the agreement between predicted and observed responses to direct and indirect selection in reported experiments. The frequency of reports of good agreement confirms the validity of the genetic theory of response to selection.

Several factors can cause poor agreement between expected and realized responses. Pešek and Baker (1971) emphasized that the parameters used in the equations for

Table 1. Agreement of predicted with observed response in selection experiments

Reference	Number of generations or cycles	Species	Selection scheme[a]	Direct (D) or Indirect (I) response	Agreement[b]
Lerner and Hazel, 1947	(12 years)	poultry	I & F	D	Good
Falconer, 1954	4,6	mouse	mass	I	Good
Frey and Horner, 1955	1	barley	lines	D	Good
Clayton et al., 1957a	7	Drosophila	I & F	I	Poor
Clayton et al., 1957b	7	Drosophila	I & F	D	Fair
Sen and Robertson, 1964	12	Drosophila	mass	I	Good
Caldwell et al., 1966	1	soybean	lines	I	Poor
Moll and Robinson, 1966	6	maize	FS	D,I	Good (D), Poor (I)
Miller and Rawlings, 1967	3	cotton	S_1	D,I	Good
Okada and Hardin, 1967	7	flour beetle	mass	D,I	Poor
Scheinberg et al., 1967	10	flour beetle	mass	D,I	Poor
Webel and Lonnquist, 1967	4	maize	MER	D	Good
Frankham et al., 1968a	12	Drosophila	mass	D	Good
Frankham et al., 1968b	50	Drosophila	mass	D	Poor
Matzinger and Wernsman, 1968	4	tobacco	mass	D,I	Good
Nickell and Grafius, 1969	1	barley	lines	D	Poor
Pešek and Baker, 1970	1	wheat	lines	D	Poor
Burton et al., 1971	4	maize	S_1, testcross	D	Poor
Moll and Stuber, 1971	6	maize	FS	D	Poor
Penny and Eberhart, 1971	5	maize	RRS	D	Poor
Darrah et al., 1972	4	maize	MER, RRS	D	Good
Rutledge et al., 1973	7	mouse	mass	I	Poor
Eagles and Frey, 1974	1	oats	lines	D,I	Poor
Berger and Harvey, 1975	10	mouse	mass	I	Good
Moll et al., 1975	1	maize	FS	D,I	Good (D), Poor (I)
Compton and Bahadur, 1977	10	maize	MER	D	Good
Eisen and Bandy, 1977	13	mouse	mass	I	Good
Rosielle et al., 1977	1	oats	lines	I	Fair
Cortez-Mendoza and Hallauer, 1979	10	maize	mass	D,I	Good
Kauffmann and Dudley, 1979	1,2	maize	HS, mass	D,I	Fair

[a]FS: Full-sib family test;
HS: Half-sib family test;
I & F: Individual and family selection;
lines: inbred line test without recombination;
mass: mass selection with recombination;
MER: Modified ear to row selection;
RRS: Reciprocal recurrent selection;
S_1: S_1 family test.

[b]Conclusion (usually that of the authors of the report) as to agreement between predicted and observed response.

predicting gains usually have large sampling variances, as do the estimates of observed gains in most experiments. Small population size is perhaps a major reason for poor agreement in some cases (e.g., Pešek and Baker, 1970).

Clayton et al. (1957a), obtained erratic responses in a correlated character. A large variation among replications suggested that drift was important. They concluded that, if the genetic correlation is low, genetic sampling in the correlated character may be the most important source of error in the estimation of its response. When selected individuals or families are intermated, genetic drift plays an important role in determining the performance level of the resulting population when traits displaying heterotic effects are involved. Inbreeding depression caused by small effective population sizes may negate the effects of selection (Smith, 1979). Genetic drift is a probable factor in some of the selection studies with maize. In the experiments described by Penny and Eberhart (1971) and Burton et al. (1971), ten S_1 lines were selected and recombined in each cycle, and observed responses were well below predicted levels. In contrast, Cortez-Mendoza and Hallauer (1979) reported unusually good agreement between expected and observed genetic changes in a mass selection experiment where 300 individuals were selected in each generation.

Frankham et al. (1968b,c) selected for bristle number in Drosophila melanogaster for 50 generations. Agreement between replications and agreement of average response with the predicted values were poorest when population size was small, indicating that drift was important. In addition, they concluded that a few genes were responsible for large effects on bristle number and that fixation of these genes by selection or drift produced apparently irregular responses. Further, linkage and epistasis could not be ruled out as contributing factors.

Moll and Robinson (1966) discussed the issue of whether to use the original data from the base population or the data from each cycle's evaluations to predict response. In their case, data from each cycle were believed to be seriously biased by genotype x environment interactions, while the data from the original population were based on a relatively broad sample of environments. They decided in favor of using the base population data in prediction equations.

Genotype x environment interaction upwardly biased the predictions of genetic response in the experiment of Eagles and Frey (1974) and was probably the major factor responsible for the particularly disappointing response to selection reported by Nickell and Grafius (1969).

Moll et al. (1975) conducted replicated studies of selection in maize for yield and ear height, using direct

and index selection. Predicted indirect responses were very different from the realized responses. Although genetic changes in component traits under index selection were more variable over replications than responses to single trait selection, there was no difference between selected traits and correlated traits in variability of response to single trait selection. Further analysis revealed that the relationship of yield and ear height was nonlinear, with an apparent optimum ear height associated with maximum yields. Nonlinear relationships between characters are not generally taken into account in prediction equations, but may be of importance.

Rutledge et al. (1973) carried out "antagonistic" index selection, in which they selected to increase one trait while decreasing a second trait that was positively correlated with the first. The progress obtained was considerably lower than predicted. The genetic correlation between the traits had previously been estimated at 0.3, but the genetic correlation realized from selection was approximately 1.0. The authors interpreted this as a result of pleiotropism and stated, "with antagonistic index selection the pleiotropic effects of genes may be more powerful in retarding response than expected".

Bohren et al. (1966) considered theoretical aspects of asymmetrical correlated responses. Asymmetry occurs when the realized response in trait 2 on selection for trait 1

is not in agreement with the response in trait 1 on selection for trait 2. The authors argued that asymmetrical responses are likely to occur, especially following simultaneous selection for the two traits. Such selection is likely to operate on loci that influence the covariance between traits. Thus, genetic covariances, more than genetic variances, may be sensitive to changes brought about by selection.

The question of whether changes in variances and covariances, occurring over cycles of selection, affect predicted progress and have a detrimental effect on the usefulness of a selection index is pertinent; however, there is no general agreement on the answer. The tendency for genetic variance to decrease with time has been noted in several recurrent selection programs (Hallauer, 1970; Burton et al., 1971; Penny and Eberhart, 1971), though not in others (Darrah et al., 1972); this may be largely the result of restricted population sizes. In the long term, selection uses up genetic variation, although the persistence of variation has been noted after 40 and 76 generations, respectively, in the investigations of Frankham et al. (1968c) and Dudley (1976).

Of great relevance to the application of index selection is the possibility of change in the genetic covariance or correlation with selection. Bohren et al. (1966) indicated that such changes were to be expected as a result of antagonistic types of selection. Friars et al. (1962) concluded

that eight years of selection for four traits in poultry had generally reduced the positive genetic correlations among the traits. Bohn and Andrus (1969), however, obtained generally favorable changes in correlations as a result of multiple trait selection. Scheinberg et al. (1967) observed that genetic covariances tended to approach zero from both directions as a result of selection, with more change in the parameters when the selection criterion was an index than when it was a single trait. Miller and Rawlings (1967) reported large changes of genetic correlations over cycles. This may have been attributable to drift, since they used very small effective population sizes. Rasmuson (1964) reported changes in correlations during fourteen generations of selection for low, but not for high, bristle number in Drosophila.

In other experiments the covariances have remained constant with selection. Frankham et al. (1968c) found no consistent change in heritabilities or phenotypic correlations during the first ten or twenty cycles of selection. Sen and Robertson (1964), in twelve generations of selection in Drosophila, and Berger and Harvey (1975), in ten generations of selection in the mouse (Mus musculus L.) observed no changes in genetic covariances.

Changes in parameters could, if they occur, require substantial changes in index weights to maintain maximum

genetic advance. The genetic gain predicted and achieved by any index, even a "parameter-free" index, depends on the parameters of the population to which it is applied. Further work is needed to answer questions such as how often a selection index must be recalculated from new estimates of the parameters, how and whether different sources of data should be pooled to yield new parameter estimates, and whether types of indices vary in their sensitivity to the changes that may occur.

Maize Protein and Protein Quality

Introduction

The protein composition of foods and feeds is of vital importance to human and animal nutrition. Thus, maize protein and its components have been the object of interest on the part of researchers for many years. An approach that was taken by some of the first scientific maize breeders was to increase the concentration of protein in the grain. The Illinois station began ear-to-row selection for high (and low) protein in the "Burr White" maize variety in 1896, and the experiment has been continued to the present time (Dudley, 1974, 1976). From an initial protein concentration of 10.9%, a concentration of 26.6% had been reached after 70 generations of selection for high protein. Successful as this

experiment has been, it has not resulted in the development and utilization of maize hybrids of superior nutritional quality. Increasing the protein content of maize grain is, by itself, insufficient for two reasons: the poor quality of maize protein for nonruminant nutrition, and the negative correlation between protein content and grain yield.

Osborne and Mendel (1914) compared zein, the principal storage protein in maize kernels, with casein and other proteins in rat (Rattus navegicus) feeding trials. Poor growth was made on a diet having zein as the sole protein source, but normal growth was obtained when zein was supplemented with tryptophan, lysine, and arginine. Subsequent work has identified lysine and tryptophan as the limiting amino acids in maize protein (Bressani, 1975).

Hansen et al. (1946) surveyed protein and zein content in a wide assortment of dent maize genotypes. They reported a correlation of 0.92 between total protein and zein content and 0.98 between endosperm protein and zein content. Frey (1951) reported a similar correlation between protein and zein content as well as a negative correlation between protein content and tryptophan content. Miller et al. (1952) found a small positive correlation between the lysine and zein concentrations in the grain but a negative correlation between protein content and lysine expressed as a proportion

of the protein (g lysine/100 g protein). Flynn et al. (1954) obtained similar results from an analysis of maize samples classified as high and low in protein. These results are consistent with the hypothesis that a genetically-based increase in protein content is expressed mainly as an increase in the low-quality zein fraction.

Increases in protein content brought about by the application of nitrogen fertilizer are similar in effect. MacGregor et al. (1961) reported that fertilization increased yield and content of protein, lysine, and tryptophan, but the proportion of lysine and tryptophan in the protein was decreased.

East and Jones stated in 1920 that "there is a certain amount of antagonism between high yield and high protein". Frey (1951) obtained correlations of yield with protein ranging from -0.03 to -0.48 in a study involving several populations. Dudley et al. (1977), working with crosses of populations from the Illinois high and low protein and oil selection program, reported a correlation of -0.70. Frey (1949), in a genetic study, found that low protein content was dominant to high protein content. This led him to suggest that hybrid vigor, as reflected in greater starch fill of kernels, was the reason for the negative correlations observed. This explanation is supported by the observation of East and Jones (1920) that seed from

open-pollinated ears had a lower concentration of protein than did seed from selfed ears. Hayes and Garber (1919) reported a negative correlation between protein content and number of seeds per ear, perhaps a result of differences between genotypes in the allocation of a limited soil nitrogen supply.

Effects of the opaque-2 allele

Many reports have suggested the existence of genetic variation for amino acid composition of maize protein (Doty et al., 1946; Frey, 1949; Wolfe and Fowden, 1957; Paez et al., 1969c). New impetus for improving protein quality, however, was provided by the discovery by Mertz et al. (1964) that the opaque-2 endosperm mutant caused a substantial (approximately 70%) increase in the content of lysine in the protein. Since that time, most of the effort in the area of protein quality improvement has been directed toward populations carrying opaque-2 or other endosperm mutants such as floury-2 (Nelson et al., 1965) and opaque-7 (Misra et al., 1972).

The opaque-2 mutant was first studied by W. R. Singleton and D. F. Jones (unpublished; cited by Emerson et al., 1935). Opaque-2 kernels differ from normal kernels in having a soft, chalky endosperm that does not transmit light. Biochemically, the opaque-2 allele suppresses the synthesis of one of the two major components of zein, the Z1 component (Lee et al.,

1976). Jones et al. (1977) observed incomplete suppression of *in vitro* Z1 synthesis by membrane-bound polysomes of opaque-2 kernels and hypothesized that the allele reduces the amount of mRNA coding for Z1. A 25% reduction from normal kernel levels of rRNA also was observed. Misra et al. (1975) reported a delay in the onset of zein synthesis in opaque-2 material as well as a lower rate of synthesis, resulting in less than half the normal zein content. In contrast to the zein storage granules present in normal maize kernels, the granules of opaque-2 kernels were found to be much smaller (Wolf et al., 1967). There is a corresponding increase in the storage of nongranular proteins in opaque-2 kernels, and in the level of free amino acids (Mertz et al., 1974).

Paez et al. (1969a) observed a modification of the opaque-2 phenotype in which opaque and translucent fractions appear in the endosperm of the same kernel. Various degrees and patterns of modification occur. According to Paez et al. (1969a), the opaque fraction of a kernel exceeded the translucent fraction in lysine content, but modified and fully opaque kernels from the same ear did not differ in lysine content because the lysine-rich germ was included in the opaque fraction. Later investigators, however, have found lysine contents of modified opaque-2 kernels to be lower than those of their opaque counterparts (Vasal, 1975;

Bauman, 1975; Bjarnason et al., 1977). Dalby and Tsai (1974) noted that a modified opaque-2 version of inbred B14 was intermediate to the normal and soft opaque versions in zein content. Similarly, Robutti et al. (1974) found modified opaque-2 protein intermediate to fully opaque and normal protein in lysine content.

The superior nutritional quality of protein from opaque-2 maize has been established in feeding trials. Mertz et al. (1975) observed protein efficiency ratios 85 and 50% as high as casein for protein from opaque-2 and normal maize, respectively. Maner (1975) concluded that opaque-2 maize could serve as the sole source of protein for swine (Sus scrofa) during the finishing, pregestation and gestation periods, protein supplements being required only during lactation and weaning. The superiority of opaque-2 maize in human nutrition has also been demonstrated (Pradilla et al., 1975). Gómez et al. (1975) found that protein from modified opaque-2 genotypes had a lower protein efficiency ratio for rat and pig nutrition than did soft opaque-2 genotypes, primarily because of the lower lysine content of the modified genotypes.

Despite its nutritional quality, opaque-2 maize has not been widely accepted by producers because of adverse effects of the opaque-2 allele on kernel traits and other

agronomic characteristics. Goodsell (1968) compared normal and opaque-2 segregants from ten crosses and found that opaque-2 kernels had smaller endosperms and less total nitrogen per kernel, but more nitrogen in the embryo. Protein concentration of the kernel was not affected by the endosperm mutant in low- and medium-protein background genotypes, but opaque-2 counterparts of normal genotypes averaging 16.1% protein had only 14.9% protein. Potassium content of opaque-2 kernels was also higher. Paez et al. (1969b) examined normal and opaque kernels from segregating ears and found that the opaque kernels were higher in moisture content at maturity and were 13% lighter than normal kernels. Nass and Crane (1970) showed that the opaque-2 allele caused a reduction in dry matter accumulation during the late grain filling period and a greater retention of moisture at harvest. Baenziger and Glover (1979) studied four hybrids in normal and opaque-2 versions and confirmed that the grain filling period ended earlier in the opaque-2 genotypes. Rate of kernel fill during the grain filling period was also lower, resulting in 18% less grain weight per ear. Cob weight also was 9% lower. Lower cob and kernel weights in opaque-2 genotypes were also reported by Makonnen and Bauman (1976). Arnold et al. (1974) found opaque-2 kernels lower than normal in total kernel and endosperm weight but higher in embryo weight.

The lighter kernel weight of opaque-2 kernels contributes to lower yields. Lambert et al. (1969) compared normal and opaque-2 versions of eight lines in crosses to two testers. Opaque-2 testcross progenies averaged 5% lower kernel weight and 8% lower yield than their normal counterparts. Opaque-2 testcrosses were associated also with a higher moisture content. Lysine content of opaque-2 testcrosses was 52% higher than normal testcrosses, with protein content slightly, but not significantly, higher. There was no difference between endosperm types in susceptibility to lodging. Sreeramulu and Bauman (1970) made similar comparisons in diallels of normal and opaque-2 lines. Yield and kernel weight were lower in the presence of opaque-2, with no difference in kernel number per ear. Protein content of opaque-2 material tended to be slightly higher than normal. Sperling (1975) tested five normal, nine soft opaque-2 and five modified opaque-2 varieties. The normal varieties averaged 13% higher yield than soft opaque-2 varieties, which in turn averaged 13% higher yield than the modified types. However, because the endosperm types were not tested in common genetic backgrounds, these results should be interpreted with caution.

In addition to lower kernel weight and yield, the altered kernel phenotype of the opaque-2 mutant gives rise to other problems in the production and processing of grain.

Lambert et al. (1969) observed an 89% higher frequency of cracked kernels in grain harvested from opaque-2 genotypes, compared to normal genotypes. Loesch et al. (1977) developed a procedure for measuring kernel hardness and found that seven normal inbreds exceeded their opaque counterparts in hardness. In a single-cross background, modified opaque-2 grain was intermediate in hardness to the normal and fully opaque types.

Kernels of opaque-2 maize are susceptible to damage by certain fungi and insects. Ullstrup (1971) reported that opaque-2 maize was severely damaged by ear-rotting fungi and that Fusarium monoliforme Sheldon seemed to be one of the dominant pathogens. Ortega et al. (1975) also found that opaque-2 maize was more susceptible than normal maize to Fusarium ear rot and reported somewhat more severe damage due to corn earworm (Heliothis zea) and sugarcane borer (Diatraea saccharalis). Insect and fungal damage were closely associated, suggestive of a synergistic effect of one pest on the other. Loesch et al. (1976) used artificial inoculation of four fungal species to compare opaque-2 and normal isolines for ear rot resistance. The opaque-2 lines were more susceptible, with Diplodia zeae (Schw.) Lev. causing more damage than F. moniliforme, Fusarium graminearum Schwabe or Nigrospora oryzae (Berk. and Br.) Petch. In contrast, Ooka and Kommedahl (1977) found no difference

between normal and opaque-2 hybrids in resistance to F. moniliforme under artificial inoculation. Vegetative fungal growth on agar medium containing corn meal was not affected by the endosperm type of the source of the meal, though sporulation was enhanced by corn meal from an opaque-2 source. Gulya (1978) identified fungal samples from 47 opaque-2 families and reported F. moniliforme as the major pathogen, with Aspergillus spp., Penicillium spp., and Rhizopus spp. also present.

Seed germination and seedling emergence are also problems associated with opaque-2 maize. Farmers in the U.S. Corn Belt have reported difficulty establishing satisfactory stands (Brown, 1975). Gupta and Kovács (1974) compared opaque-2 and normal versions of several lines and hybrids for emergence at cold temperatures. The opaque material was inferior in emergence in all genetic backgrounds. Even with the application of fungicides, emergence of opaque-2 maize was at best 68% that of untreated normal maize. Loesch et al. (1978) compared normal and opaque-2 kernels from segregating ears for emergence traits. Normal genotypes had higher emergence percentages, emerged more rapidly, and had higher seedling dry weights than their opaque-2 counterparts. There was significant genetic variation in the opaque population for these traits.

Other differences between normal and opaque-2 maize

have been noted. Opaque-2 genotypes were slightly higher in oil content in the experiments reported by Lambert et al. (1969), and a difference in fatty acid composition has been reported (Arnold et al., 1974). Gupta and Kovács (1978) observed that leaf area index of opaque-2 genotypes was 2.4% less than that of normal counterparts, a factor which was considered to contribute to differences in yield. Salamini et al. (1970) compared hybrids in opaque-2 and normal endosperm for several plant traits. Opaque hybrids tended to have shorter and narrower leaves. There were no differences in plant and ear height, date of pollen shed, and ear length and diameter. Frost treatments of two-week-old seedlings revealed a difference in reaction of the two endosperm types (Gupta and Kovács, 1976). Opaque-2 seedlings were more susceptible to damage and had lower fresh and dry weights and fewer leaves than comparable normal seedlings. Differences in frost tolerance seemed to be independent of variation for germinability.

Most studies of differences between opaque-2 and normal maize have been aimed at determining the "average" effect of the opaque-2 allele in a number of genetic backgrounds. However, the genetic background may itself be an important factor interacting with endosperm type effects. For example, Lambert et al. (1969) reported that two opaque-2 hybrids significantly outyielded their normal counterparts,

although on the average the normal hybrids were superior. Feist and Lambert (1970) followed changes in g lysine/100 g protein as six lines were converted to opaque-2 by backcrossing. The rate of change in protein quality with generations of backcrossing varied from line to line, indicating a background effect. There was no such variation for kernel weight. Significant interactions between endosperm type and the genetic background however, were observed by Makonnen and Bauman (1976) for kernel weight, Sreeramulu and Bauman (1970) for kernel weight and yield, and Loesch et al. (1976) for ear rot resistance.

Carañgal (1975) summarized the needs for improvement in opaque-2 maize: increased yields, harder endosperm, better milling recovery, greater resistance to pests and diseases, and a faster drying rate. The importance of yield and disease resistance is obvious. A harder endosperm would be useful in decreasing fungal damage (Ortega et al., 1975); also, soft endosperm types are discriminated against in many maize-consuming societies where protein deficiencies occur (Poey, 1975).

Inheritance and selection in opaque-2 maize

Many researchers have investigated the inheritance of agronomic and protein quality traits in opaque-2 maize. Several studies have used a diallel of five to ten fixed

lines to compare general (GCA) and specific (SCA) combining ability effects (Sreeramulu and Bauman, 1970; Paez and Zuber, 1973a,b; Gupta et al. 1975; Bjarnason et al., 1977; Singh et al., 1977; Gulya, 1978). In general, GCA effects were significant and exceeded SCA effects for lysine and protein content, g lysine/100 g protein, test weight, kernel weight, kernel breakage, kernel specific gravity, moisture content, and ear rot resistance.

Baker (1978) has questioned the validity of heritability estimates obtained from such diallels; nevertheless, these results are consistent with conclusions from more extensive studies that most of these traits have medium to high heritabilities. Dudley et al. (1975) obtained heritability estimates (averaged over two opaque-2 synthetics and three cycles of selection) of 0.33 for lysine, 0.16 for g lysine/100 g protein, 0.84 for protein, and 0.54 for yield. Motto (1979) reported heritabilities of 0.62 for tryptophan content, 0.27 for g tryptophan/100 g protein, 0.68 for protein, 0.80 for yield,0.80 for moisture content, and 0.70 for kernel specific gravity in a modified opaque-2 synthetic. Demopulos-Rodriguez (1977) reported estimates of 0.65 for lysine, 0.60 for g lysine/100 g protein, 0.76 for protein, 0.57 for yield, 0.77 for moisture content, and 0.88 for kernel weight. (All the above heritabilities are reported on a family mean basis. The experiment of Dudley et al., 1975, included

evaluation of each population at a single location, and consequently genotype x environment interaction is a source of bias. The other experiments were conducted in more than one environment.) Vasal (1975) reported success in transferring modified opaque-2 characteristics by backcrossing; he concluded that kernel opacity was highly heritable.

Results of the diallel experiment of Bjarnason et al. (1976) are consistent with this conclusion. Loesch et al. (1976) measured kernel hardness in two sets of S_2 lines from an opaque-2 synthetic and obtained heritability estimates of 0.77 and 0.88. Choe et al. (1976) crossed normal maize selections with high and low lysine contents to opaque-2 material. They found that the levels of lysine were transmitted to the opaque-2 progeny, indicative of a polygenically inherited genetic system affecting lysine content, operating independently of opaque-2 and apparently capable of producing considerable heritable variation for lysine content within an opaque-2 population.

Correlations involving agronomic and protein quality traits have been reported (Table 2). The negative correlation between protein and yield, observed also in normal maize, has been consistently reported in opaque-2 maize. The negative correlation between yield and lysine content can probably be attributed in part to the same cause--starch

Table 2. Phenotypic and genotypic (in parentheses) correlations reported in opaque-2 maize

Reference	YLD-PROT[a]	YLD-LYS	YLD-LP	YLD-LYLD
Sreeramulu & Bauman, 1970	.06	-.07	-.16	.71
Dudley et al., 1971				
Synth. Ao_2, C0	-.38	-.08	.09	.84
Synth. Ao_2, C1	-.38	-.14	.09	.79
Dudley et al., 1975				
Synth. SSSSo_2, C0	-.30 (-.47)	-.02 (.22)	.17 (.72)	.75 (.82)
Synth. SSSSo_2, C1	-.34 (-.43)	-.24 (-.39)	-.07 (-.17)	.80 (.87)
Synth. SSSSo_2, C2	-.21 (-.27)	-.12 (-.57)	.01 (-.05)	.93 (.99)
Synth. DOo_2, C0	-.27 (-.37)	-.06 (.05)	.14 (.62)	.78 (.81)
Synth. DOo_2, C1	-.34 (-.49)	-.29 (-.60)	-.09 (-.51)	.82 (.92)
Synth. DOo_2, C2	-.20 (-.26)	-.07 (-.14)	.09 (.16)	.94 (.96)
Paez and Zuber, 1973a,b				
Gupta et al., 1975	-.68	-.77	-.53	.96
Arnold et al., 1977				
Ind. o_2 Synth. A				
Ill. Synth. 60D x testers				
Bjarnason et al., 1977				
Demopulos-Rodriguez, 1977	-.23 (-.23)	-.24 (-.29)	-.07 (-.13)	

[a]YLD: grain yield; PROT: protein content; LYS: grain lysine content; LP: g lysine/100 g protein; LYLD: yield of lysine per unit area; KWT: weight per 100 kernels.

LYLD-LYS	PROT-LYS	PROT-LP	LYS-LP	KWT-PROT	KWT-LYS	KWT-LP
.65	.67	.10	.70	-.05	-.06	-.11
.46	.14	-.30	.90			
.49	.47	-.14	.80			
.64 (.74)	.41 (.57)	-.20 (-.32)	.81 (.60)			
.39 (.12)	.55 (.90)	.01 (.34)	.84 (.72)			
.24 (-.47)	.33 (1.01)	-.34 (-1.21)	.77 (-1.44)			
.57 (.62)	.51 (.77)	-.17 (-.20)	.76 (.48)			
.30 (-.23)	.57 (1.00)	-.09 (-.08)	.76 (.04)			
.26 (.14)	.59 (.81)	-.26 (-.19)	.67 (.42)			
	.68 (.80)	-.51 (-.44)	.28 (.17)	-.16 (-.43)	-.18 (-.33)	-.16 (-.43)
	.90	.24	.64	-.89	-.86	-.01
	.83	-.33	.25	-.11	-.01	.16
	.70	-.12	.62	.01	-.01	.00
	.86	-.24	.28	-.20	-.20	-.08
	.69 (.72)	-.31 (-.34)	.47 (.41)	-.21 (-.23)	-.22 (-.28)	-.08 (-.13)

accumulation increasing yield and diluting the nitrogenous compounds. Yield and g lysine/100 g protein have a correlation near zero in most experiments. Yield of lysine per unit area is more closely associated with grain yield than with lysine concentration. The correlations involving protein, lysine, and g lysine/100 g protein indicate that as protein content increases, the incremental protein is relatively poorer in lysine. The correlations involving kernel weight are similar to the corresponding correlations with yield.

Dudley et al. (1975) selected for lysine yield in two opaque-2 synthetics. There is some indication that certain correlations were changed as a result of selection (Table 2). Negative relationships appeared or were strengthened between yield and lysine and between lysine yield and lysine. The correlation between yield and lysine yield increased nearly to unity.

Paez and Zuber (1973a) found that the percentage of broken kernels in a harvested sample was positively correlated with g lysine/100 g protein and negatively correlated with lysine and protein content and kernel specific gravity. According to Gulya (1978), ear rot resistance was associated with high yield, kernel hardness, specific gravity, and moisture content and with low lysine and g lysine/100 g protein. The correlations reported by Demopulos-Rodriguez

(1977) will be discussed further in the Results and Discussion section of this dissertation.

Few have measured lysine and tryptophan in the same experiment. Alexander et al. (1970) reported that the two traits seemed uncorrelated. However, Motto (1979) obtained correlations of -0.36 tryptophan with yield, 0.75 for tryptophan with protein, 0.08 for g tryptophan/100 g protein with yield, and -0.51 for g tryptophan/100 g protein with protein which were similar to the corresponding correlations for lysine.

Selection programs involving opaque-2 maize have emphasized improving the yield of grain, lysine, or tryptophan. Bauman (1970) used a population heterozygous for +/opaque-2 to select for small differences in weight between normal and opaque-2 kernels on the same selfed ear. Three cycles of selection produced a small increase in the weight of opaque kernels but a large decline in that of normal kernels. Dudley et al. (1975) used half-sib family testing to select for lysine yield in two opaque-2 synthetics. Lysine yield was increased approximately 8 to 14% during two cycles, with most of the improvement in the first cycle. Most of the advance was in grain yield with a small increase in g lysine/100 g protein. Lysine and protein content changed very little.

Motto et al. (1978) discussed breeding methods for

selection to improve tryptophan yield in opaque-2 maize. Assuming one growing season per year, they predicted that full-sib selection would provide greater gain per year than either mass or half-sib selection. They suggested testing full-sibs in two locations with two replications per location and predicted a gain of 32% of the base population mean per cycle.

MATERIALS AND METHODS

Field Experiments

Data employed in this study were obtained in three experiments, a design II experiment (Comstock and Robinson, 1952) and experiments 77107 and 78105. Plant materials for all three experiments were derived from the maize population BSAAo_2 (Loesch, 1979), a broad-based opaque-2 synthetic that originated from a recurrent selection study being conducted for improvement of grain yield, protein quality and other agronomic traits. Material from the design II experiment and from experiment 77107 was derived from BSAAo_2(S)C1, while the lines used in experiment 78105 came from BSAAo_2(S)C2, which resulted from an additional cycle of selection for yield and protein quality in BSAAo_2(S)C1.

The procedures used in the design II experiment were reported in detail by Demopulos-Rodriguez (1977); a brief description will be given here. One hundred twelve full-sib families, divided into seven sets of sixteen entries, were developed by crossing four randomly chosen plants as males to four randomly chosen females within each set. The 112 families were evaluated in 1975 under two levels of nitrogen fertilizer application (0 and 112 kg/ha) at two locations (the Agronomy Farm and the Animal Science Farm, both near Ames, Iowa). There were two replications at each

location. Plots consisted of two rows 5m long spaced 102 cm apart. Planting and harvesting were done by hand.

Data were collected on the following characters:

1) grain yield (YLD), measured in quintals/hectare;

2) grain moisture content at harvest (MOIST), determined on a Steinlite Electronic Moisture tester;

3) weight, in g, of 300 random kernels (KWT);

4) kernel specific gravity (SPGRAV), determined by measuring the water displacement (in cm^3) in a graduated cylinder of the 300-kernel sample used for KWT, and then using the formula

$$SPGRAV = \frac{KWT}{\text{water displacement}};$$

5) ear rot score (ER), rated visually on a scale ranging from 1.0 (free of infection) to 5.0 (severe infection);

6) kernel hardness (KH), measured with a shear press on a 10g sample from each plot, as described by Loesch et al. (1976);

7) grain protein content (PROT), determined by micro-Kjeldahl methods and expressed as a percentage of kernel weight;

8) grain lysine content (LYS), determined on a Beckman Automatic Amino Acid Analyzer and expressed as a percentage of kernel weight;

9) g lysine/100 g protein, or lysine content of the protein (LP), determined by the formula

$$LP = \frac{LYS}{PROT} \times 100;$$

10) grain histidine content[1] (HIST), determined on a Beckman Automatic Amino Acid Analyzer and expressed as a percentage of kernel weight;

[1]Histidine, though an essential amino acid, is not considered a limiting factor in the nutritional quality of maize protein. It is measured automatically during the lysine assay and was included for consideration in this study as a correlated character with no economic value of its own.

11) g histidine/100 g protein, or histidine content of the protein (HP), determined by the formula

$$HP = \frac{HIST}{PROT} \times 100;$$

12) yield of protein (PYLD) in kg/ha, determined by PYLD = YLD x PROT;

13) yield of lysine (LYLD) in kg/ha, determined by LYLD = YLD x LYS;

14) opacity score (OPAC), the visually estimated percentage of a sample of kernels that did not transmit light when placed over a light source; both number of modified kernels and degree of modification were considered; a fully opaque sample was given a score of 100, while a score less than 100 indicated the presence of kernel modification;

15) test weight (TWT) in pounds/bushel, determined by weighing a one-quart container full of grain on a standard test weight scale;

16) kernel quality (KQUAL), a visual score of the plumpness of kernels in a sample; a scale of 1.0 (good quality kernels) to 5.0 (extremely shrunken, malformed kernels) was used;

17) kernel fracture (KFRACT), a visual score on a scale of 1.0 (no cracked or broken kernels) to 5.0 (severely cracked kernels).

Traits 7 through 11, referred to collectively as the "protein traits" were determined by Dr. W. J. Wiser, USDA-SEA, Beltsville, Md.

Individual plant data were determined in experiment 78105. Twenty random S_1 lines were machine-planted May 10, 1978, at Ames, Iowa, in a randomized complete block design with three replications. Each plot included two rows 5m long spaced 76cm apart. A density of 49,100 plants/ha was obtained by thinning. It had been intended to harvest random

plants in each plot, but severe ear rotting necessitated restricting the harvested sample to six relatively disease-free ears from each plot. Measurements of PROT, LYS, LP, and OPAC were made on each ear, using the procedures outlined for the design II experiment. A sample of 100 kernels was counted and weighed and the weight multiplied by 3 to determine KWT. Kernel hardness was determined on a manual shear press, similar to the electronic shear press used to determine KH in other experiments. Two 7-gram samples from each ear were measured, and the mean, expressed in m-kg, was identified as KHM.

Additional individual plant data were obtained in experiment 77107. Approximately 6000 open-pollinated S_0 plants were grown in isolation at the Agronomy Farm near Ames, Iowa, in 1976. Ears were harvested from 577 plants that had been visually selected for plant characters and freedom from ear rotting. The mean KH of two 10-gram samples from each ear was determined as in the design II experiment.

Statistical Analysis and Parameter Estimates

A separate analysis of variance for each set-nitrogen level combination of the design II experiment was obtained using the model

$$Y_{ghi} = \mu + L_g + R_{gh} + G_i + (GL)_{gi} + e_{ghi},$$

where

$g = 1,2;$

$h = 1,2;$

$i = 1,2,\ldots,16;$

and

Y_{ghi} = the measurement of the i^{th} genotype in the h^{th} replication at the g^{th} location;

μ = the population mean;

L_g = the effect attributable to the g^{th} location;

R_{gh} = the effect attributable to the h^{th} replication at the g^{th} location;

G_i = the effect attributable to the i^{th} genotype;

$(GL)_{gi}$ = the interaction of the i^{th} genotype with the g^{th} location;

e_{ghi} = the experimental error.

The i^{th} genotype can be regarded as the progeny of the cross between the j^{th} male and the k^{th} female, so that a further partition is possible:

$$G_i = G_{i(jk)} = M_j + F_k + (MF)_{jk},$$

where

$j = 1,2,3,4;$

$k = 1,2,3,4;$

and

M_j = the effect attributable to the j^{th} male;

F_k = the effect attributable to the k^{th} female; and

$(MF)_{jk}$ = the interaction of the j^{th} male and the k^{th} female.

Similarly,

$$(GL)_{gi} = (GL)_{gi(jk)} = (ML)_{gj} + (FL)_{gk} + (MFL)_{gjk},$$

where

$(ML)_{gj}$ = the interaction of the g^{th} location with the j^{th} male;

$(FL)_{gk}$ = the interaction of the g^{th} location with the k^{th} female; and

$(MFL)_{gjk}$ = the three-way interaction.

The analysis of variance table constructed from this model is given in Table 3.

Estimates of M_M, M_F, M_{MF}, M_{ML}, M_{FL}, M_{MFL}, and M_e for use in estimating genetic parameters were obtained by pooling over sets and nitrogen levels, e.g.,

$$M_M = \frac{1}{14}(M_{M_{1,1}} + M_{M_{1,2}} + M_{M_{2,1}} + \ldots + M_{M_{1,2}})$$

where

$M_{M_{s,t}}$ = the estimate of M_M obtained from the s^{th} set and the t^{th} nitrogen level.

The expectations of mean squares (Table 3) permit variance components to be estimated as follows:

$$S^2_M = \frac{1}{rfl}(M_M + M_{MFL} - M_{MF} - M_{ML}),$$

$$S^2_F = \frac{1}{rml}(M_F + M_{MFL} - M_{MF} - M_{FL}),$$

$$S^2_{MF} = \frac{1}{rl}(M_{MF} - M_{MFL}),$$

Table 3. Analysis of variance for one set-nitrogen level combination of the design II experiment

Source	df[a]	Mean square	Expectation of mean square
Locations (L)	$\ell-1$	M_L	
Replications/L	$\ell(r-1)$	$M_{R/L}$	
Genotypes (G)	$mf-1$	M_G	
Males (M)	$m-1$	M_M	$\sigma^2 + r\sigma^2_{MFL} + r\ell\sigma^2_{MF} + rf\sigma^2_{ML} + rf\ell\sigma^2_M$
Females (F)	$f-1$	M_F	$\sigma^2 + r\sigma^2_{MFL} + r\ell\sigma^2_{MF} + rm\sigma^2_{FL} + rm\ell\sigma^2_F$
M x F	$(m-1)(f-1)$	M_{MF}	$\sigma^2 + r\sigma^2_{MFL} + r\ell\sigma^2_{MF}$
G x L	$(mf-1)(\ell-1)$	M_{GL}	
M x L	$(m-1)(\ell-1)$	M_{ML}	$\sigma^2 + r\sigma^2_{MFL} + rf\sigma^2_{ML}$
F x L	$(f-1)(\ell-1)$	M_{FL}	$\sigma^2 + r\sigma^2_{MFL} + rm\sigma^2_{FL}$
M x F x L	$(m-1)(f-1)(\ell-1)$	M_{MFL}	$\sigma^2 + r\sigma^2_{MFL}$
Error	$\ell(r-1)(mf-1)$	M_e	σ^2
Total	$rmf\ell-1$		

[a] r,m,f, = number of replications, males, females, and locations, respectively.

$$S^2_{ML} = \frac{1}{rf}(M_{ML} - M_{MFL}),$$

$$S^2_{FL} = \frac{1}{rm}(M_{FL} - M_{MFL}),$$

$$S^2_{MFL} = \frac{1}{r}(M_{MFL} - M_e),$$

$$S^2_e = M_e.$$

The derivation of the genetic components of variance involves the following assumptions (Comstock and Robinson, 1952):

1) male and female parents randomly chosen from the population;

2) regular diploid behavior at meiosis;

3) random distribution of genotypes relative to variation in the environment;

4) no maternal effects on plant traits or pollen parent effects on seed traits;

5) linkage equilibrium in the source population;

6) no epistasis.

There is no reason to believe that assumptions 1, 2 and 3 were invalid in this experiment. Xenia effects on protein and kernel quality traits are possible but probably of minor importance. Deviations from linkage equilibrium were probably minimized by the intermating process used in developing the population. Sprague and Eberhart (1977) stated that epistasis was of limited importance in random-mating maize populations.

The derivation of the genetic interpretation of variance components follows the argument of Mode and Robinson (1959). Absence of linkage disequilibrium and of epistasis permits consideration of the contribution of each locus individually. Let there be a locus $\underline{B}$ with an arbitrary number of alleles $\underline{B}_i$. Let p_i be the frequency of the i^{th} allele and Y_{ij} be the genotypic value, expressed as a deviation from the population mean, corresponding to the $\underline{B}_i\underline{B}_j$ genotype. Then the additive effect of the i^{th} allele is given by

$$\alpha_i = \sum_j p_j Y_{ij}$$

and the dominance deviations are

$$\delta_{ij} = Y_{ij} - \alpha_i - \alpha_j.$$

The additive and dominance components of variance are given by

$$\sigma_A^2 = 2\sum_i p_i \alpha_i^2$$

and

$$\sigma_D^2 = \sum_i \sum_j p_i p_j \delta_{ij}^2.$$

The following results facilitate computation:

1) $\sum_i p_i \alpha_i = \sum_i \sum_j p_i p_j Y_{ij}$ = population mean of $Y_{ij} = 0$;

2) For all j, $\sum_i p_i\delta_{ij} = \sum_i p_i(Y_{ij} - \alpha_i - \alpha_j)$

$= \sum_i p_iY_{ij} - \sum_i p_i\alpha_i - \alpha_j$

$= \alpha_j - \alpha_j = 0;$

3) By 2), $\sum_i \sum_j p_ip_j\alpha_i\delta_{ij} = \sum_i p_i\alpha_i \sum_j p_j\delta_{ij} = \sum_i p_i\alpha_i \cdot 0 = 0;$

and

4) By 2), $\sum_i \sum_j p_ip_j\delta_{ij}\delta_{ik} = \sum_i p_i\delta_{ik} \sum_j p_j\delta_{ij} = 0.$

Now, let $\underline{B}_r\underline{B}_s$ be the genotype of a male parent and $\underline{B}_u\underline{B}_v$ be the genotype of a female parent. The mean genotypic value of the crossed progeny is then $\frac{1}{4}(Y_{ru} + Y_{su} + Y_{rv} + Y_{sv})$, and the effect attributable to the male parent is, since $\sum_u p_u = \sum_v p_v = 1$,

$$M = \frac{1}{4}\sum_u \sum_v p_up_v(Y_{ru} + Y_{su} + Y_{rv} + Y_{sv})$$

$$= \frac{1}{4}\sum_u p_u(Y_{ru} + Y_{su} + \sum_v p_vY_{rv} + \sum_v p_vY_{sv})$$

$$= \frac{1}{4}(\sum_u p_uY_{ru} + \sum_u p_uY_{su} + \sum_v p_vY_{rv} + \sum_v p_vY_{sv})$$

$$= \frac{1}{4}(2\alpha_r + 2\alpha_s) = \frac{1}{2}(\alpha_r + \alpha_s).$$

The population mean of male effects is zero, so that the variance among male effects is given by

$$\sigma_M^2 = \sum_r \sum_s p_r p_s [\tfrac{1}{2}(\alpha_r+\alpha_s)]^2$$

$$= \tfrac{1}{4} \sum_r p_r \sum_s p_s(\alpha_r^2 + 2\alpha_r\alpha_s + \alpha_s^2)$$

$$= \tfrac{1}{4} \sum_r p_r(\alpha_r^2 + 2\alpha r \sum_s p_s\alpha_s + \sum_s p_s\alpha_s^2).$$

By 1),

$\sum_s p_s\alpha_s = 0$, so that

$\sigma_M^2 = \frac{1}{4}(\sum_r p_r\alpha_r^2 + \sum_s p_s\alpha_s^2) = \frac{1}{4}(\frac{1}{2}\sigma_A^2 + \frac{1}{2}\sigma_A^2) = \frac{1}{4}\sigma_A^2$.

By the symmetry of the mating design, it is clear that $\sigma_F^2 = \frac{1}{4}\sigma_A^2$.

The variance component for males x females, σ_{MF}^2, is given by

$$\sigma_{MF}^2 = \sigma_G^2 - \sigma_M^2 - \sigma_F^2.$$

The variance σ_G^2 can be expressed in terms of genetic parameters as

$$\sigma_G^2 = \frac{1}{16} \sum_r \sum_s \sum_u \sum_v p_r p_s p_u p_v(2\alpha_r + 2\alpha_s + 2\alpha_u + 2\alpha_v + \delta_{ru} + \delta_{sv} + \delta_{rv} + \delta_{su})^2,$$

by expanding the genotypic mean $\frac{1}{4}(Y_{ru} + Y_{su} + Y_{rv} + Y_{sv})$ in terms of α's and δ's.

Squaring,

$$\sigma_G^2 = \frac{1}{16} \sum_r \sum_s \sum_u \sum_v p_r p_s p_u p_v (4\alpha_r^2 + 4\alpha_s^2 + 4\alpha_u^2 + 4\alpha_v^2 + \delta_{ru}^2 + \delta_{su}^2$$

$$+ \delta_{rv}^2 + \delta_{sv}^2 + 4\alpha_r\delta_{ru} + 4\alpha_r\delta_{su} + 4\alpha_r\delta_{rv} + 4\alpha_r\delta_{sv}$$

$$+ 4\alpha_s\delta_{ru} + 4\alpha_s\delta_{su} + 4\alpha_s\delta_{rv} + 4\alpha_s\delta_{sv} + 4\alpha_u\delta_{ru}$$

$$+ 4\alpha_u\delta_{su} + 4\alpha_u\delta_{rv} + 4\alpha_u\delta_{sv} + 4\alpha_v\delta_{ru} + 4\alpha_v\delta_{su}$$

$$+ 4\alpha_v\delta_{rv} + 4\alpha_v\delta_{sv} + 8\alpha_r\alpha_s + 8\alpha_r\alpha_u + 8\alpha_r\alpha_v$$

$$+ 8\alpha_s\alpha_u + 8\alpha_s\alpha_v + 8\alpha_u\alpha_v + 2\delta_{ru}\delta_{su} + 2\delta_{ru}\delta_{rv}$$

$$+ 2\delta_{ru}\delta_{sv} + 2\delta_{su}\delta_{ru} + 2\delta_{su}\delta_{sv} + 2\delta_{rv}\delta_{sv}).$$

This expression is simplified by summing over v, u, s, and r in turn and using 1, 2, 3 and 4:

$$\sigma_G^2 = \frac{1}{16} \sum_r \sum_s \sum_u p_r p_s p_u (4\alpha_r^2 + 4\alpha_s^2 + 4\alpha_u^2 + 2\sigma_A^2 + \delta_{ru}^2 + \delta_{su}^2$$

$$+ \sum_v p_v\delta_{rv}^2 + \sum_v p_v\delta_{sv}^2 + 4\alpha_r\delta_{ru} + 4\alpha_r\delta_{su} + 4\alpha_s\delta_{ru}$$

$$+ 4\alpha_s\delta_{su} + 4\alpha_u\delta_{ru} + 4\alpha_u\delta_{su} + 4\sum_v p_v\alpha_v\delta_{rv}$$

$$+ 4\sum_v p_v\alpha_v\delta_{sv} + 8\alpha_r\alpha_s + 8\alpha_r\alpha_u + 8\alpha_s\alpha_u$$

$$+ 2\delta_{ru}\delta_{su} + 2\sum_v p_v\delta_{rv}\delta_{su})$$

$$= \frac{1}{16} \sum_r \sum_s p_r p_s (4\alpha_r^2 + 4\alpha_s^2 + 4\sigma_A^2 + \sum_u p_u \delta_{ru}^2 + \sum_u p_u \delta_{su}^2$$

$$+ \sum_v p_v \delta_{rv}^2 + \sigma_D^2 + 4 \sum_u p_u \alpha_u \delta_{ru} + 4 \sum_u p_u \alpha_u \delta_{su}$$

$$+ 4 \sum_v p_v \alpha_v \delta_{rv} + 4 \sum_v p_v \alpha_v \delta_{sv} + 8\alpha_r \alpha_s$$

$$+ 2 \sum_u p_u \delta_{ru} \delta_{su} + 2 \sum_v p_v \delta_{rv} \delta_{sv})$$

$$= \frac{1}{16} \sum_r p_r (4\alpha_r^4 + 6\sigma_A^2 + \sum_u p_u \delta_{ru}^2 + 2\sigma_D^2 + \sum_v p_v \delta_{rv}^2$$

$$4 \sum_u p_u \alpha_u \delta_{ru} + 4 \sum_v p_v \alpha_v \delta_{rv})$$

$$= \frac{1}{16}(8\sigma_A^2 + 4\sigma_D^2)$$

$$= \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2.$$

Consequently,

$$\sigma_{MF}^2 = \sigma_G^2 - \sigma_M^2 - \sigma_F^2 = \frac{1}{4}\sigma_D^2.$$

It is similarly shown that $\sigma_{ML}^2 = \sigma_{FL}^2 = \frac{1}{4}\sigma_{AL}^2$ and $\sigma_{MFL}^2 = \frac{1}{4}\sigma_{DL}^2$.

Estimates of genetic parameters were obtained from variance components as follows:

$$s_A^2 = 2(s_M^2 + s_F^2)$$

$$s_D^2 = 4s_{MF}^2$$

$$s_{AL}^2 = 2(s_{ML}^2 + s_{FL}^2)$$

$$s^2_{DL} = 4s^2_{MFL}.$$

Negative estimates of s^2_{AL} or s^2_{DL} were obtained for some traits; where this occurred the value 0 was substituted for purposes of calculating phenotypic variances.

Genetic components of covariances were obtained in an analogous manner from cross-products analyses of each pair of traits (Mode and Robinson, 1959).

Additive genetic correlations between all pairs of traits X and Y were determined using

$$r_{A;X,Y} = \frac{s_{A;X,Y}}{\sqrt{(s^2_{A;X})(s^2_{A;Y})}}$$

where

$s_{A;X,Y}$ = the additive component of covariance between X and Y, and

$s^2_{A;X}$ and $s^2_{A;Y}$ = the additive genetic variance for X and Y, respectively.

The plot mean data from experiment 78105 were analyzed using the model for a randomized complete block experiment:

$$\bar{Y}_{ij.} = \mu + R_i + G_j + e_{ij},$$

where

$i = 1,2,3;$

$j = 1,2,\ldots,20;$

$\bar{Y}_{ij.}$ = the mean of 6 plants of the j^{th} genotype, measured in the i^{th} replication;

μ = the experiment mean;

R_i = the effect attributable to the i^{th} replication;

G_j = the effect attributable to the j^{th} genotype;

and

e_{ij} = the experimental error.

Data were missing from four plots; missing values were supplied and degrees of freedom adjusted as indicated by Cochran and Cox (1957, p. 110).

Individual plant data were used to calculate the within-plot variance:

$$s_w^2 = \frac{1}{56} \sum_{k=1}^{56} \frac{1}{n_k - 1} \sum_{\ell=1}^{n_k} (Y_{k\ell} - \bar{Y}_k)^2,$$

where

n_k = the number of plants measured in plot k;

$Y_{k\ell}$ = the measurement on the ℓ^{th} plant in the k^{th} plot;

and

$\bar{Y}_{k.}$ = the mean for the k^{th} plot.

The analysis of variance table for experiment 78105 is given in Table 4. F tests for significance of replication and genotype effects were made as follows:

for replication effects, $F = \frac{M_R}{M_e}$,

and for genotype effects, $F = \frac{M_G}{M_e}$.

The variance component for genotypes, $s_G^2 = (M_G - M_e)/r$ (where r = the harmonic mean of the number of replications

Table 4. Analysis of variance for experiment 78105

Source	df[a]	Mean square	Expectation of mean square
Replications[b]	r-1	M_R	$\sigma_e^2 + \frac{1}{n}\sigma_w^2 + g\sigma_r^2$
Genotypes[b]	g-1	M_G	$\sigma_e^2 + \frac{1}{n}\sigma_w^2 + r\sigma_g^2$
Error[b]	(r-1)(g-1)	M_e	$\sigma_e^2 + \frac{1}{n}\sigma_w^2$
Within plots[c]	rg(n-1)	M_w	σ_w^2

[a] r,g,n = number of replications, genotypes, and plants per plot, respectively.

[b] Based on plot means.

[c] Based on individual plant measurements.

per genotype) is an estimate of the additive genetic variance. Though possibly biased by dominance effects and genotype x environment interaction and based on a limited sample of lines, s_G^2 was calculated so that comparisons could be made between genetic variances from 78105 and those from the design II experiment. The sampling variance of s_G^2, determined using the formula from Mode and Robinson (1959), is

$$\begin{aligned} \mathrm{Var}(s_G^2) &= \mathrm{Var}\left[\frac{1}{r}(M_G - M_e)\right] \\ &= \frac{1}{r^2}\left[\mathrm{Var}(M_G) + \mathrm{Var}(M_e)\right] \\ &= \frac{1}{r^2}\left[\frac{2M_G^2}{g+1} + \frac{2M_e^2}{(r-1)(g-1)+2}\right]. \end{aligned}$$

Within-plot covariances between all pairs of traits, X, Y, were calculated as follows:

$$s_{w;X,Y} = \frac{1}{56} \sum_{k=1}^{56} \frac{1}{n_k - 1} \sum_{\ell=1}^{n_k} (X_{k\ell} - \bar{X}_{k.})(Y_{k\ell} - \bar{Y}_{k.})$$

where,

n_k = number of plants in plot k measured in both X and Y;

$X_{k\ell}$, $Y_{k\ell}$ = measurements of X and Y, respectively, on the ℓ^{th} plant in the k^{th} plot;

and

$\bar{X}_{k.}$, $\bar{Y}_{k.}$ = mean in X, Y, respectively, for the k^{th} plot.

Correlations between pairs of traits, X, Y, were determined on a within-plot basis by means of the formula

$$r_{w;X,Y} = \frac{s_{w;X,Y}}{\sqrt{(s^2_{w;X})(s^2_{w;Y})}} .$$

The among-plant variance, s^2_p, for KH was determined from the data in experiment 77107 as follows:

$$s^2_p = \frac{1}{576}\left[\sum_i \bar{X}^2_{i.} - \left(\sum_i \bar{X}_{i.}\right)^2\right]$$

where i = 1,2,...,577; and $\bar{X}_{i.}$ = the mean KH (over two determinations) for i^{th} plant. The sampling variance of s^2_p was estimated by

$$\mathrm{Var}(s^2_p) = \frac{2s^4_p}{df+2} ,$$

where df = 576.

Four recurrent selection schemes were investigated in this study (Table 5). Phenotypic variances pertinent to each type of selection were calculated by using the design II parameter estimates in the formulas given by Empig et al. (1972) and Sprague and Eberhart (1977):

$$s^2_{P(S_1)} = s^2_A + \frac{1}{4}s^2_D + \frac{1}{\ell}(s^2_{AL} + \frac{1}{4}s^2_{DL}) + \frac{1}{r\ell}\, s^2_e;$$

$$s^2_{P(FS)} = \frac{1}{2}s^2_A + \frac{1}{4}s^2_D + \frac{1}{\ell}(\frac{1}{2}s^2_{AL} + \frac{1}{4}s^2_{DL}) + \frac{1}{r\ell}\, s^2_e;$$

$$s^2_{P(S_2)} = \frac{3}{2}s^2_A + \frac{3}{16}\, s^2_D + \frac{1}{\ell}(\frac{3}{2}\, s^2_{AL} + \frac{3}{16}\, s^2_{DL}) + \frac{1}{r\ell}\, s^2_e.$$

Phenotypic covariances were estimated in analogous fashion from the covariance components. Progeny testing at two locations with two replications per location was assumed throughout this study.

According to Robinson et al. (1949), the error component can be further subdivided, as

$$\sigma^2_e = \frac{E_w + G_w}{n} + E_P$$

where

E_w = environmental variance among plants in the same plot;

G_w = genetic variance among plants in the same plot;

n = number of plants per plot;

E_p = environmental variance among plots.

The term G_w and hence also σ^2_e would vary depending on the

Table 5. Summary of recurrent selection schemes investigated

Method	Year	Season[a]	Location[b]	Procedure
S_1 testing (2 years/cycle)				
	1	S	I	Recombine selected lines
	1-2	W	WN	Self to produce S_1 lines
	2	S	I	Test S_1 lines
S_1 testing (3 years/cycle)				
	1	S	I	Recombine selected lines
	2	S	I	Self to produce S_1 lines
	3	S	I	Test S_1 lines
Full-sib testing				
	1	S	I	Make plant-to-plant crosses among selected families
	2	S	I	Test full-sib families
S_2 testing				
	1	S	I	Recombine selected lines
	1-2	W	WN	Make second recombination
	2	S	I	Self to produce S_1 generation
	3	S	I	Self to produce S_2 lines
	4	S	I	Test S_2 lines

[a] S = summer, W = winter.

[b] I = Iowa, WN = winter nursery location.

type of family being tested. A common error estimate, s_e^2, was used in the study for all recurrent selection schemes, however, since the contribution of G_w to σ_e^2 would be small in relation to that of E_w and E_p.

The coefficients of the s_D^2 and s_{DL}^2 terms in the expressions for $s_{P(S_1)}^2$ and $s_{P(S_2)}^2$ are correct only if two alleles, each with frequency $\frac{1}{2}$, are assumed at each locus.[1] Otherwise, the coefficients cannot be simply defined.

Phenotypic correlations between pairs of traits, X, Y, were determined using the formula

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[1]The derivation of the genetic variance among lines under these assumptions is as follows: in an inbred population let genotypes BB, Bb, and bb have genotypic value as shown.

genotype	frequency	value
BB	$\frac{1}{4}(1+F)$	a
Bb	$\frac{1}{2}(1-F)$	d
bb	$\frac{1}{4}(1+F)$	-a

The mean among selfed progeny from this population is $\frac{1}{4}(1-F)$, while the variance among selfed progeny is given by

$$V = \tfrac{1}{4}(1+F)a^2 + \tfrac{1}{2}(1-F)(\tfrac{1}{2}d)^2 + \tfrac{1}{4}(1+F)a^2 - [\tfrac{1}{4}d(1-F)]^2$$
$$= \tfrac{1}{2}(1+F)a^2 + \frac{1}{16}(1-F^2)d^2.$$

But, in terms of the original noninbred population, $\sigma_A^2 = \frac{1}{2}a^2$ and $\sigma_D^2 = \frac{1}{4}d^2$, so that

$$V = (1+F)\sigma_A^2 + \tfrac{1}{4}(1-F^2)\sigma_D^2.$$

In particular, for S_1 lines, $F = 0$ and $V = \sigma_A^2 + \frac{1}{4}\sigma_D^2$, while for S_2 lines,

$$F = \tfrac{1}{2} \text{ and } V = \frac{3}{2}\sigma_A^2 + \frac{3}{16}\sigma_D^2.$$

$$r_{P;X,Y} = \frac{s_{P;X,Y}}{\sqrt{(s^2_{P;X})(s^2_{P;Y})}},$$

where

$s_{P;XY}$ = the phenotypic covariance between X and Y;

and

$s^2_{P;X}$, $s^2_{P;Y}$ = the phenotypic variances of X and Y, respectively.

Heritabilities pertinent to each breeding scheme were calculated for each trait as follows:

$$h^2_{(S_1)} = \frac{s^2_A}{s^2_{P(S_1)}},$$

$$h^2_{(FS)} = \frac{\frac{1}{2}s^2_A}{s^2_{P(FS)}},$$

and

$$h^2_{(S_2)} = \frac{\frac{3}{2}s^2_A}{s^2_{P(S_2)}}.$$

If two alleles, B and b, with frequencies p and q, respectively, are assumed at each locus and if in addition there is no environmental correlation among measurements of plants in the same plot, then the genetic variance among S_1 plants within an S_1 line can be determined from the general formula of Gates et al. (1957):

$$\sigma^2_{G_{w_1}} = \frac{1}{2}\sigma^2_A + \frac{1}{2}\sigma^2_D.$$

Under these assumptions the phenotypic variance among plants within a plot, as estimated in experiment 78105, would be

$$\sigma^2_{P_{w_1}} = \frac{1}{2}\sigma^2_A + \frac{1}{2}\sigma^2_D + \frac{1}{2}\sigma^2_{AL} + \frac{1}{2}\sigma^2_{DL} + \sigma^2$$

where

σ^2 = the environmental variance among plants in the same plot.

In order to calculate responses to selection among individual S_0 plants, the phenotypic variance among S_0 plants ($\sigma^2_{P(S_0)} = \sigma^2_A + \sigma^2_D + \sigma^2_{AL} + \sigma^2_{DL} + \sigma^2$) is required. A direct estimate for KH was available from experiment 77107. For PROT, LYS, LP, OPAC, and KWT, estimates of $\sigma^2_{P(S_0)}$ were obtained by adding $\frac{1}{2}(s^2_A + s^2_D + s^2_{AL} + s^2_{DL})$ to the within-plot variance estimate from 78105. The term $\frac{1}{2}(s^2_A + s^2_D + s^2_{AL} + s^2_{DL})$ was estimated from the design II experiment. Covariances, except those involving KH, on an S_0 plant basis were estimated similarly, i.e., $\frac{1}{2}(s_{A;XY} + s_{D;XY} + s_{AL;XY} + s_{DL;XY})$ was added to the within-plot covariance between X and Y that had been estimated from experiment 78105.

Covariances involving KH could not be obtained by this method since KH was not measured in experiment 78105. To obtain these estimates, it was assumed that the correlation of a trait X, with KHM (which was measured in experiment 78105) would be equal to the corresponding correlation with KH. Thus, the covariance with KH, $s_{P(S_0);KH,X}$ could be

determined by using

$$s_{P(S_0);KH,X} = (r_{w;KHM,X})\sqrt{(s^2_{w:KH})(s^2_{P(S_0);X})}$$

where $s^2_{w;KH}$ came from experiment 77107.

For the S_2 recurrent selection scheme, selection among individual S_1 plants was considered. The phenotypic variance among such plants, $\sigma^2_{P_{a_1}}$, on the assumption that each S_0 ancestor is represented by no more than one S_1 plant, is $\frac{3}{2}\sigma^2_A + \frac{3}{4}\sigma^2_D + \frac{3}{2}\sigma^2_{AL} + \frac{3}{4}\sigma^3_{DL} + \sigma^2$ (Gates et al., 1957). To obtain estimates of $\sigma^2_{P(S_1)}$, the value $s^2_A + \frac{1}{4}s^2_D + s^2_{AL} + \frac{1}{4}s^2_{DL}$ was added to the within-plot variance estimate for 78105. Covariances were estimated similarly, except that covariances involving KH were determined using

$$s_{P_{a_1};KH,X} = r_{w;KHM,X}\sqrt{(s^2_{P_{a_1};KH})(s^2_{P_{a_1};X})},$$

where $s^2_{P(S_1);KH}$ was estimated by adding to the among-S_0 variance estimate from 77107 the value $\frac{1}{2}s^2_A - \frac{1}{4}s^2_D + \frac{1}{2}s^2_{AL} - \frac{1}{4}s^2_{DL}$, estimated in the design II.

Falconer (1960, pp. 318-322) defined the efficiency, E, of indirect selection as the ratio of the expected gain in X on selection for Y to the expected gain from direct selection in X:

$$E = \frac{kh_Y|r_A|\sigma_{A;X}}{kh_{X\ A;X}} = \frac{h_Y}{h_X}|r_A|,$$

where h_Y and h_X represent the square roots of the heritabilities of Y and X, respectively, and r_A is the genetic correlation between X and Y. The absolute value of r_A is used because selection for low values of Y can be used to increase X if the correlation is negative.

Calculation of Selection Indices

The theory of index selection was originally given by Smith (1936) and Hazel (1943). The following development is, in its essentials, that of Lin (1978).

The selection index, I, and aggregate genotype, H, are defined as

$$I = \sum_{i=1}^{n} b_i x_i = \underline{x}'\underline{b}$$

$$H = \sum_{i=1}^{n} a_i g_i = \underline{g}'\underline{a},$$

where $\underline{x}' = (x_1 x_2 \ldots x_n)$, $\underline{g}' = (g_1 g_2 \ldots g_n)$, $\underline{a}' = (a_1 a_2 \ldots a_n)$, and $\underline{b}' = (b_1 b_2 \ldots b_n)$ are row vectors with

x_i = the measurement (phenotype) for the i^{th} trait;

g_i = the unknown genotypic value for the i^{th} trait;

a_i = the "economic" weight for the i^{th} trait;

and

b_i = the index coefficient or weight to be computed.

Thus, it is desired to improve H by selecting on I.

The phenotypic (P) and genetic (G) variance-covariance matrices are assumed to be known:

$$P = \begin{bmatrix} \sigma^2_{P;1} & \sigma_{P;1,2} & \cdots & \sigma_{P;1,n} \\ \sigma_{P;2,1} & \sigma^2_{P;2} & \cdots & \sigma_{P;2,n} \\ \vdots & \vdots & & \vdots \\ \sigma_{P;n,1} & \sigma_{P;n,2} & \cdots & \sigma^2_{P;n} \end{bmatrix}$$

and

$$G = \begin{bmatrix} \sigma^2_{G;1} & \sigma_{G;1,2} & \cdots & \sigma_{G;1,n} \\ \sigma^2_{G;2,1} & \sigma^2_{G;2} & \cdots & \sigma_{G;2,n} \\ \vdots & \vdots & & \vdots \\ \sigma^2_{G;n,1} & \sigma_{G;n,2} & \cdots & \sigma^2_{G;n} \end{bmatrix}$$

where $\sigma^2_{P;i}$ and $\sigma^2_{G;i}$ are phenotypic and genetic variances of trait i and $\sigma_{P;i,j}$ and $\sigma_{G;i,j}$ are phenotypic and genetic covariances of traits i and j.

From these, the variances and covariances involving I and H are calculated:

$$\sigma^2_I = \sum_{i=1}^{n} \sum_{j=1}^{n} b_i b_j P_{ij} = \underline{b}' P \underline{b}'$$

$$\sigma^2_H = \sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j G_{ij} = \underline{a}' G \underline{a};$$

and

$$\sigma_{HI} = \sum_{i=1}^{n} \sum_{j=1}^{n} a_i b_j G_{ij} = \underline{b}' G \underline{a}.$$

Absence of correlation between genotype and environment has

been assumed in the derivation of the expression for σ_{HI}.

The genetic gain, ΔH, in H on selection for I is determined by use of the regression equation

$$\Delta H = (\bar{I}_s - \bar{I}_\mu)b_{HI},$$

where $\bar{I}_\mu$ and $\bar{I}_s$ are mean index scores of the population and selected individuals, respectively, and b_{HI} is the regression coefficient of H on I. If $k = (\bar{I}_s - \bar{I}_\mu)/\sigma_I$, the standardized selection differential, then

$$\Delta H = k\sigma_I b_{HI}.$$

The correlation between H and I is given by $r_{HI} = \frac{\sigma_{HI}}{\sigma_H \sigma_I}$, while $b_{HI} = \frac{\sigma_{HI}}{\sigma_I^2} = \frac{\sigma_H}{\sigma_I} r_{HI}$, so that

$$\Delta H = k\sigma_H r_{HI}.$$

For maximum genetic vain, therefore, it is desired to determine the index weights (i.e., the vector $\underline{b}$) that maximize r_{HI}. Now,

$$r_{HI} = \frac{\underline{b}'G\underline{a}}{(\underline{b}'P\underline{b})^{\frac{1}{2}}(\underline{a}'G\underline{a})^{\frac{1}{2}}}$$

so that $\log r_{HI} = \log(\underline{b}'G\underline{a}) - \frac{1}{2}\log(\underline{b}'P\underline{b}) - \frac{1}{2}\log(\underline{a}'G\underline{a})$. The value of $\underline{b}$ that maximizes r_{HI} also maximizes $\log r_{HI}$, and this value is determined by differentiation:

$$\frac{\partial \log r_{HI}}{\partial \underline{b}} = \frac{1}{\underline{b}'G\underline{a}} G\underline{a} - \frac{1}{2}\frac{1}{\underline{b}'P\underline{b}} \cdot 2P\underline{b} = 0,$$

and

$$\underline{Pb} = \underline{Ga}\,\frac{\underline{b}'\underline{Pb}}{\underline{b}'\underline{Ga}}\,.$$

Only the proportionality of the b_i's, not their absolute values, is important. The scalar $\frac{\underline{b}'\underline{Pb}}{\underline{b}'\underline{Ga}}$ can therefore be dropped, and the solution becomes

$$\underline{Pb} = \underline{Ga}$$

or

$$\underline{b} = P^{-1}\underline{Ga}.$$

Only restricted selection indices were used in this study. A restricted index is designed to maximize aggregate gain subject to specified restrictions. Restrictions may be of two types: 1) restrictions on the coefficients of the index (including the important special case where a coefficient equals zero, i.e., there is no information on a trait); and 2) restrictions on the gain in certain traits. The solution presented by James (1968) was employed in this study, and a specialized development of this method follows.

Let r of the n index coefficients be required to have the value 0, so that the index incorporates information only from the remaining n-r traits. These restrictions can be written

$$\sum_{j=1}^{n} K_{ij}b_j = 0$$

where i = 1,2,...,r. Alternatively, matrix notation can be used, with K as the r x n matrix of elements K_{ij}. The restrictions then become

$$K\underline{b} = 0.$$

Let there be s additional restrictions that genetic changes in linear functions $\sum_{j=1}^{n} C_{ij}g_j$ be 0. If C is the s x n matrix with elements C_{ij}, then the restrictions can be written as

$$CG\underline{b} = 0.$$

To solve for $\underline{b}$, let I be the n x n identity matrix and Q be the result of vertically joining K and CG:

$$Q = \begin{pmatrix} K \\ CG \end{pmatrix}.$$

The solution is then

$$\underline{b} = [I - P^{-1}Q'(QP^{-1}Q')^{-1}Q]P^{-1}G\underline{a}.$$

For a solution to exist, it is necessary that desired restrictions be attainable. For example, if trait 1 is uncorrelated with all other traits and it is specified that $b_1 = 0$, then genetic change in trait 1 is impossible. It is also necessary that r+s be less than n and that $QP^{-1}Q'$ be nonsingular.

As an example of the specification of restrictions in matrix form, let n = 5 and suppose gains in traits 1 and 2

are required to be in the ratio 10:1 while the genetic value for trait 3 is left unchanged. Further, let the index incorporate only traits 1, 3, 4, and 5. Then r = 1, s = 2,

$$K = [0 \quad 1 \quad 0 \quad 0 \quad 0],$$

and

$$C = \begin{bmatrix} -1 & 10 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{bmatrix},$$

For purposes of this study, YLD was considered to be the only trait having economic value. Restrictions were used to ensure genetic gain in KH and LP. For the major portion of the investigation, gains in YLD, KH, and LP were restricted to the proportion 200:24:1. This ratio was arbitrary, but its use resulted in a satisfactory balance of gains. In addition, restrictions that gain in MOIST or PROT be zero were applied when MOIST would increase or PROT decrease from use of an index lacking such restrictions.

For arbitrary values of $\underline{b}$, the genetic response in the i^{th} trait on selection for $I = \underline{x}'\underline{b}$ is

$$\Delta g_i = (\bar{I}_s - \bar{I}_\mu) b_{g_i I},$$

where $b_{g_i I}$ is the coefficient of regression of g_i on I. On substitution of matrix values, this becomes the genetic gain formula of Finney (1962):

$$\Delta g_i = \frac{k\sigma_{g_i I}}{\sigma_I}$$

$$= \frac{k \sum_{j=1}^{n} b_j G_{ij}}{\sigma_I}$$

$$= \frac{k(G\underline{b})_i}{\sqrt{\underline{b}'P\underline{b}}} ,$$

where $(G\underline{b})_i$ is the i^{th} element of the column vector $G\underline{b}$.

In particular, if direct selection is practiced on trait j, $b_j = 1$ and $b_\ell = 0$ for $\ell \neq j$, and the gain in trait j is

$$\Delta g_j = \frac{k\sigma^2_{G;J}}{\sigma_{P;J}} ,$$

while the gain in trait ℓ, $\ell \neq j$, is

$$\Delta g_\ell = \frac{k\sigma_{G;j\ell}}{\sigma_{P;j}} .$$

A selection intensity of 20% (k = 1.40) was used throughout this study.

The procedure used for calculating the sampling variance of the expected gain is presented in Appendix A.

Since the determination of expected gain in this study was based on the formulas for gain from recurrent selection that were presented by Empig et al. (1972), the assumptions required in their derivation are implicit. These assumptions include:

1) normal diploid behavior at meiosis;

2) linkage equilibrium;

3) no multiple alleles;

4) no epistasis;

5) normal distribution of phenotypes;

6) true truncation selection;

7) linear regression of allele frequency on phenotype.

The integration of index selection and the different recurrent selection schemes was achieved by using appropriate family bases for the genetic and phenotypic variances and covariances. Since selected families were to be recombined, only the additive portion of the genetic variance or covariance was pertinent. Thus, the elements of the genetic variance-covariance matrix for S_1, full-sib, and S_2, testing were, respectively, 1, $\frac{1}{2}$, and $\frac{3}{2}$ times the design II estimates for the corresponding additive variances and covariances.[1] The phenotypic variances and covariances were calculated as shown on p. 62.

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[1]The additive portion of the genetic variance (or covariance) among S_1 or S_2 lines contains a term, C, that cannot be expressed in terms of genetic parameters (Empig et al., 1972). C equals 0 if gene frequencies are 1/2 (assuming two alleles per locus) or if dominance is not present. For this study, C was assumed to be 0. This assumption is a source of bias in the estimate of gain, but, since dominance was of relatively little importance for most traits, the amount of bias would be small.

Coefficients of each index were divided by the absolute value of the coefficient for YLD to facilitate comparison of the coefficients of different indices. Consequently, the weight for YLD in every index was 1 or -1.

Hill and Thompson (1978) reported that an index calculated using a genetic variance-covariance matrix that was nonpositive-definite [i.e., that had at least one negative eigenvalue (Hohn, 1973, pp. 375-381)], may not be valid. A negative eigenvalue corresponds to a negative estimate of the genetic variance of a linear combination of the traits in the index. Accordingly, the eigenvalues of genetic variance-covariance matrices corresponding to combinations of traits that were used in selection indices were examined. Eigenvalues were determined by means of a computer subroutine (Barr et al., 1976).

For an index of n traits, the corresponding n x n submatrix of the full genetic variance-covariance matrix was investigated with respect to eigenvalues. This submatrix contained only the rows and columns associated with the traits of the index. No eigenvalue determination was made, however, for an index that produced low expected gains (i.e., an index in the lower 50% among indices of the same type[1] having the same number of traits).

[1]See p.101 of Results and Discussion for definition of index types.

Signs of the eigenvalues of a matrix are not affected by multiplication of the matrix by a positive scalar. Since the genetic variance-covariance matrices for full-sib and S_2 testing were, respectively, 1/2 and 3/2 times that for S_1 testing, it was sufficient to determine eigenvalues for S_1 matrices only.

The magnitude of an index weight depends on the unit in which a trait is measured. Comparison of the weights of different traits within a given index requires consideration of the patterns of variability of each trait. For this reason, the importance of trait x_j relative to trait x_i in an index was defined by

$$R_{ji} = \left|\frac{b_j}{b_i}\right| \frac{s_{P;j}}{s_{P;i}}$$

where

b_k = the index coefficient for trait x_k, $k = 1,2,\ldots,n$, and

$s_{P;k}$ = the phenotypic standard deviation for trait x_k.

This definition is justified by the following argument (in which, without loss of generality, the index weights are assumed to be positive). Let A and B be two families and let x_{kA} and x_{kB} be, respectively, the phenotypes of A and B in trait x_k. Also, let I_A and I_B be, respectively, the index scores for A and B. Then, if A exceeds B by m phenotypic standard deviation units in x_i, measurements for all

other traits being equal, it follows that

$$x_{iA} - x_{iB} = ms_{P;i},$$

and

$$I_A - I_B = \sum_k b_k(X_{kA}-X_{kB}) = mb_i s_{P;i} .$$

If, instead, A exceeds B by m phenotypic standard deviation units in trait x_j,

$$x_{jA} - x_{jB} = ms_{P;j},$$

and

$$I_A - I_B = mb_j s_{P;j} = mR_{ji} b_i s_{P;i} .$$

Thus, the difference in index score in the second case is R_{ji} times that in the first case. In this sense, x_j contributes more, equally, or less than x_i to the index score according as R_{ji} is greater than, equal to, or less than unity. An extension of the definition in which traits x_i and x_j are taken as linear combinations of component traits can be made.

If the weights of an index assign equal relative importance to all traits, then the index can be written

$$I = b_1x_1 + b_2x_2 + \ldots + b_nx_n,$$

or, equivalently, dividing each term by $b_1 s_{P;1}$,

$$I = \frac{1}{s_{P;1}} x_1 + \frac{b_2}{b_1 s_{P;1}} x_2 + \ldots + \frac{b_n}{b_1 s_{P;1}} x_n$$

$$= \frac{1}{s_{P;1}} x_1 + \frac{1}{s_{P;2}} R_{21} x_2 + \ldots + \frac{1}{s_{P;n}} R_{n_1} x_n$$

$$= \frac{1}{s_{P;1}} x_1 + \frac{1}{s_{P;2}} x_2 + \ldots + \frac{1}{s_{P;n}} x_n ,$$

which is the base-standard deviation index suggested by Subandi et al. (1973) and Crosbie et al. (p. 10, herein).

Incorporation of individual plant data into selection indices was achieved by enlarging the genetic and phenotypic variance-covariance matrices to include individual plant traits. The form of the genetic variance-covariance matrix, G, when p traits were determined with progeny data and q traits on individual plants was as follows:

$$G = \left[\begin{array}{c|c} G_{11} & G_{12} \\ \hline G_{21} & G_{22} \end{array}\right]$$

where

G_{11} = the p x p matrix of additive genetic variances and covariances used to calculate indices incorporating progeny data only;

G_{12} = the p x q matrix consisting of additive genetic covariances between traits measured in progeny tests and traits measured on individual plants. Specifically, the element in the i^{th} row and j^{th} column of G_{12} was the covariance between the i^{th} progeny trait (i=1,2,...,p) and the j^{th} individual plant trait (j=1,2,...,q);

$G_{21} = G_{12}'$;

and

G_{22} = the q x q matrix consisting of additive genetic variances and covariances of individual plant traits.

Similarly, the phenotypic variance-covariance matrix was as follows:

$$P = \left[\begin{array}{c|c} P_{11} & P_{12} \\ \hline P_{21} & P_{22} \end{array}\right]$$

where

P_{11} = the p x p phenotypic variance-covariance matrix used to calculate indices incorporating progeny data only;

P_{12} = the p x q matrix consisting of phenotypic covariances between traits measured in progeny tests and traits measured on individual plants. The element in the i^{th} row and j^{th} column of P_{12} was the phenotypic covariance between the i^{th} progeny trait and the j^{th} individual plant trait.

$P_{21} = P_{12}'$;

and

P_{22} = the q x q matrix consisting of phenotypic variances and covariances of individual plant traits.

The elements of P_{12} and G_{12} were obtained by using the expectation of the covariances in terms of parameter estimates available from the analysis of the design II experiment. The phenotypic covariance between trait x_i, measured on the S_0 plant, and trait x_j, determined as the mean of the

S_1 progeny, is $\sigma_{A;ij} + \frac{1}{2}\sigma_{D;ij}$. If x_i is measured on an S_1 plant and x_j on the S_2 progeny, the covariance between x_i and x_j is $\frac{3}{2}\sigma_{A;ij} + \frac{3}{8}\sigma_{D;ij}$. The covariance when x_i is determined on an S_0 plant and x_j on the full-sib progeny is $\frac{1}{2}\sigma_{A;ij}$. Derivations of these expressions are given in Appendix B.

These phenotypic covariances include no environmental components because the environments of a plant and its progeny are uncorrelated. Only the additive portions of the covariance are used in G_{12}. Thus, for S_1 testing supplemented by S_0 plant data, $(G_{12})_{ij} = s_{A;ij}$; for S_2 testing with S_1 plant data, $(G_{12})_{ij} = \frac{3}{2}s_{A;ij}$; and for full-sib testing with individual plant data, $(G_{12})_{ij} = (P_{12})_{ij} = \frac{1}{2}s_{A;ij}$.

For S_1 testing or full-sib testing, the elements $(G_{22})_{ij}$ of G_{22} were taken as $s_{A;ij}$ (or $s^2_{A;i}$ for diagonal elements). For S_2 testing, $(G_{22})_{ij} = \frac{3}{2}s_{A;ij}$.

The elements of P_{22} were the estimates of $s_{P;ij}$ or $s^2_{P;i}$ on the appropriate single plant basis, i.e., among S_0 plants for S_1 and full-sib testing, and among S_1 plants for S_2 testing.

For a given recurrent selection scheme, the n x n genetic variance-covariance submatrix associated with a combination of n traits was the same whether the traits were measured on single plants or in replicated progeny tests. Therefore, if a combination of traits had been eliminated

because it gave rise to nonpositive-definite genetic variance-covariance matrices in pure progeny testing, it was also eliminated from consideration for progeny-individual plant testing.

In conjunction with investigations of selection indices incorporating individual plant data, the possibility of culling individual plants based on a portion of the index was examined. The amount of space, labor, and expense assocaited with replicated progeny testing is more likely to limit progress from plant breeding than the resource requirement for growing and evaluating single plants. It would be advantageous, therefore, to evaluate more single plants than could be progeny-tested and to use single plant measurements to discard plants unlikely to have high index scores.

An index, I, of individual plant and replicated progeny traits can be partitioned into two components, I_p and I_r, representing linear combinations of traits measured on individual plants and in replicated progeny tests, respectively. It is assumed that I_p and I_r follow a bivariate normal distribution with means μ_p and μ_r, variances σ_p^2 and σ_r^2, and covariance σ_{pr}.

Selection is to be based on $I = I_p + I_r$, and the mean and variance of I are

$$\mu_I = \mu_p + \mu_r$$

and

$$\sigma_I^2 = \sigma_p^2 + 2\sigma_{pr} + \sigma_r^2.$$

Let q be the proportion of progeny actually tested that are selected, and let z_q satisfy the condition that the probability that a standard normal variate falls above z_q is q, i.e., $\Phi(z_q) = 1-q$. Then, progenies for which the value of I is greater than $L = \mu_I + z_q\sigma_I$ will be selected.

The problem is to determine a level K for culling on I_p. The risk of discarding an individual plant that would produce a progeny worthy of selection must be considered. Accordingly, a protection level, α, is chosen such that the probability that I>L given that $I_p = K$ is α. In probability notation,

$$P(I>L|I_p=K) = \alpha.$$

The conditional distribution of I_r, given that $I_p = K$, is normal with mean and variance

$$\mu_{I_r|I_p=K} = \mu_r + \beta(K-\mu_p),$$

and

$$\sigma^2_{I_r|I_p=K} = \sigma_r^2(1-\rho^2) \text{ (Lindgren, 1976, p. 470)},$$

where

$$\rho = \frac{\sigma_{pr}}{\sigma_p\sigma_r}, \text{ the correlation of } I_p \text{ with } I_r,$$

and

$$\beta = \frac{\sigma_{pr}}{\sigma_p^2}$$, the coefficient of regression of I_r on I_p.

It is assumed that $\beta > -1$, for otherwise an increase of one unit in I_p is associated with a decrease of at least one unit in I_r and consequently no net increase in $I = I_p + I_r$. Selection for low values of I_p would be called for if $\beta < -1$.

If z_α denotes the value such that $\Phi(z_\alpha) = 1-\alpha$, then, given $I_p = K$, I_r will, with probability $1-\alpha$, be less than $\mu_{I_r|I_p=K} + z_\alpha \sigma_{I_r|I_p=K}$, and $I = I_p + I_r$ will, with the same probability, be less than $K + \mu_{I_r|I_p=K} + z_\alpha \sigma_{I_r|I_p=K}$. K must, therefore, satisfy

$$K + \mu_{I_r|I_p=K} + z_\alpha \sigma_{I_r|I_p=K} = L$$

that is,

$$K + \mu_r + \beta(K-\mu_p) + z_\alpha \sigma_r \sqrt{1-\rho^2} = L$$

so that

$$K = \frac{L-\mu_r+\mu_p\beta-z_\alpha\sigma_r\sqrt{1-\rho^2}}{1+\beta}$$

$$= \mu_p + \frac{z_q\sigma_I - z_\alpha\sigma_r\sqrt{1-\rho^2}}{1+\beta}$$

The value of K was determined for each index by setting $q = .20$ (i.e., 20% selection intensity among progenies) and using protection levels $\alpha = .05$, .10, and .25. Estimates

of σ_p^2, σ_r^2, and σ_{pr} were calculated from the known index weights and the estimates of phenotypic variances and covariances of component traits. Trait means were assumed to be those of the design II experiment, except that, where mean YLD of inbred plants was required, a component Δ, due to inbreeding depression, was subtracted from the mean YLD of the design II experiment.[1] Traits other than YLD were not adjusted for inbreeding depression. All indices studied had $\beta > -1$.

After the value of K had been determined for each index and protection level, the proportion, $s = P(I_p < K)$, of individual plants that could be discarded was determined by using the estimates for μ_p and σ_p and referring to a table of the standard normal distribution. It was assumed that 100 progenies could be evaluated in replicated trials, so that $\frac{100}{1-s}$ individual plants could be evaluated. Expected gain was calculated for the resulting effective selection intensity of $20(1-s)\%$.

Two factors would probably contribute to upward bias in these expected gain estimates:

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[1] For two alleles per locus and notation as on p. 204, the mean of S_0 plants is $a(p-q) + 2pqd$, and means of S_1 plants (or lines) and S_2 lines are, respectively, $a(p-q) + pqd$ and $a(p-q) + \frac{1}{2}pqd$. Therefore $\Delta = pqd = \frac{1}{2}\sqrt{\sigma_D^2}$ for S_1 plants and $\Delta = \frac{3}{2}pqd = \frac{3}{4}\sqrt{\sigma_D^2}$ for S_2 lines

1) failure of true truncation selection because of the possibility of discarding individual plants that should have been saved; the magnitude of bias introduced by this factor would increase with α; and

2) failure to adjust variances and covariances for the effects of individual plant selection; selection would decrease genetic variances, particularly if $|\rho|$ or s were large, and reduce progress from selection among progenies. The coefficients of the optimum selection index, however, would not be affected by such changes in the parameters (Cunningham, 1975).

RESULTS AND DISCUSSION

Results of Field Experiments

The results of the design II experiment were discussed in detail by Demopulos-Rodriguez (1977) (see Appendix C for estimates of variance and covariance components). Additive genetic and phenotypic correlations are given in Table 6. Heritability estimates are given in Table 7.

The negative correlation between ER and LYS and the near-zero correlation between ER and LP contrast with the positive correlations obtained by Gulya (1978). Otherwise, the correlations reported here are consistent with those reported in previous experiments with opaque-2 maize (Table 2, p. 40 and p. 42). Likewise, the heritability estimates are consistent with those reported previously (p. 38), except for the low estimate for SPGRAV.

The analysis of variance and other pertinent data from experiment 78105 are given in Table 8. Differences among families were highly significant for all traits. The among-family variance component, an estimate of the additive genetic variance, was within approximately one standard error of the estimate of σ_A^2 from the design II experiment for five of the six traits. The among-family variance component for OPAC was nearly three times as large as the design II estimate. There are several possible reasons for this discrepancy. The variance component estimates from 78105 could

Table 6. Additive genetic (above diagonal) and phenotypic (below diagonal) correlations for traits measured in the design II experiment

Trait	TRAIT									
	YLD	MOIST	KWT	SPGRAV	ER	KH	PROT	LYS	LP	
YLD	-	-.19	.38	-.14	-.41	-.34	-.33	-.28	-.01	-.43
MOIST	-.22	-	.11	.13	-.15	.45	.29	.07	-.27	.35
KWT	.21	.05	-	.05	.11	.16	-.14	-.25	-.16	-.12
SPGRAV	-.10	-.01	.00	-	.02	.24	-.09	-.45	-.49	.34
ER	-.22	-.20	.10	-.07	-	-.34	-.30	-.32	-.02	-.10
KH	-.14	.29	.09	.18	-.19	-	.53	.11	-.67	.46
PROT	-.18	.18	-.15	-.02	-.17	.37	-	.79	-.29	.90
LYS	-.19	.03	-.20	-.18	-.11	.09	.67	-	.37	.80
LP	-.05	-.14	-.08	-.14	.06	-.33	-.32	.48	-	-.12
HIST	-.27	.22	-.10	-.11	-.04	.32	.75	.80	.15	-
HP	-.14	.06	.04	-.12	.12	-.08	-.27	.22	.61	.44
PYLD	.80	-.11	.11	-.10	-.29	.04	.34	.15	.21	.13
LYLD	.79	-.20	.09	-.20	-.27	-.10	.21	.38	.24	.12
OPAC	.05	-.09	.24	-.33	.16	-.43	-.09	.29	.53	.05
TWT	.01	.13	-.02	.46	-.19	.44	.11	-.21	-.41	-.07
KQUAL	-.20	-.12	-.41	-.04	.07	-.15	.01	.16	.20	.10
KFRACT	-.08	-.11	.12	-.08	.43	-.23	-.18	.06	.29	.04

TRAIT						
HP	PYLD	LYLD	OPAC	TWT	KQUAL	KFRACT
-.29	.77	.74	.14	-.04	-.42	-.30
.29	.01	-.15	-.08	.15	-.23	-.18
-.01	.26	.18	.39	-.05	-.63	.23
-.50	-.25	-.48	-.66	.74	-.19	.02
.26	-.57	-.60	.13	-.16	.16	.82
-.16	-.02	-.31	-.69	.70	-.45	-.21
-.14	.36	.23	-.17	.16	.08	-.24
.07	.24	.41	.20	-.20	.38	.00
.34	-.20	.26	.59	-.55	.45	.41
.52	.20	.15	-.09	-.09	.33	.18
-	-.35	-.21	.19	-.50	.51	.76
-.27	-	.90	.03	.13	-.34	-.42
.00	.85	-	.28	-.22	-.14	-.22
.17	.00	.22	-	-.79	-.08	.36
-.24	-.10	-.12	-.60	-	-.43	-.47
.13	-.19	-.09	-.03	-.33	-	.11
.27	-.16	-.03	.25	-.33	.09	-

Table 7. Heritability estimates from the design II experiment, expressed on the basis of S_1, full-sib, and S_2 family means

Trait	Heritability		
	S_1 family basis	Full-sib family basis	S_2 family basis
YLD	0.50	0.37	0.60
MOIST	0.85	0.75	0.90
KWT	0.90	0.82	0.93
SPGRAV	0.33	0.19	0.43
ER	0.71	0.55	0.80
KH	0.60	0.46	0.69
PROT	0.76	0.62	0.84
LYS	0.67	0.52	0.75
LP	0.56	0.40	0.67
HIST	0.74	0.59	0.82
HP	0.45	0.30	0.54
PYLD	0.49	0.36	0.58
LYLD	0.51	0.37	0.60
OPAC	0.72	0.57	0.84
TWT	0.79	0.65	0.87
KQUAL	0.56	0.42	0.66
KFRACT	0.49	0.34	0.59

Table 8. Analysis of variance, means, and genetic variance estimates from experiment 78105

Source	df	HIST Mean square	df	LYS Mean square	df	PROT Mean square
Replications	2	.002487**	2	.001807	2	.565
Families	19	.001562**	19	.001763**	19	1.277**
Error	34	.000364	34	.000647	34	.356
Within plots	274	.000928	278	.001477	278	.737
Mean		.281%		.349%		8.81%
$\hat{\sigma}^2_g$ (s.e.)[a]		.000439 (.000184)		.000409 (.000212)		.337 (.151)
$\hat{\sigma}^2_A$[b]		.000242		.000564		.2973

[a]Among-family variance component (with standard error in parentheses).

[b]Estimate of additive genetic variance from design II experiment, shown for purposes of comparison.

**$P < .01$.

	LP		OPAC		KHM
df	Mean square	df	Mean square	df	Mean square
2	.1194**	2	416.3**	2	1.917**
19	.1254**	19	320.8**	19	2.479**
34	.0202	34	69.7	34	.312
278	.0701	274	347.0	274	1.805
	3.96 g/100 g		85.6%		8.50 m-kg
	.0385 (.0146)		92.0 (37.6)		.794 (.288)
	.0364		31.40		-

be biased by dominance effects, or, since evaluation was in a single environment, by genotype x environment interaction. Alternatively, since the lines in 78105 were from cycle 2 of BSAAo2 while the design II material came from cycle 1, selection for modified opaque kernels could have increased genetic variance for this trait by increasing the previously low frequencies of genes for modification.

Within-plot components of covariance and correlation coefficients are given in Table 9. Most of the correlations were similar to those obtained in the design II experiment. Correlations involving KHM were similar to the corresponding values for KH, except for that between KHM and LP, which was smaller than the correlation between KH and LP.

Estimates of the single-plant heritability relevant to mass selection of S_0 plants were determined using the estimates of additive genetic variance from the design II experiment and an estimate of the phenotypic variance among S_0 plants (calculated as shown on p. 66) (Table 10). The value for OPAC may be an underestimate because of the discordant additive genetic variance estimates obtained from the design II and the plot-mean analysis of 78105.

Covariance estimates for S_0 traits that were used in matrices for index calculation are shown in Appendix C.

The mean value of KH for the S_0 plants measured in experiment 77107 was 56.1, and the variance among plants

Table 9. Within-plot components of covariance (above diagonal) and correlations (below diagonal) among traits measured in experiment 78105

Trait	Trait					
	HIST	LYS	PROT	LP	OPAC	KHM
HIST	-	.000955	.0214	.00110	-.0108	.0159
LYS	.82	-	.0260	.00476	.1044	.0104
PROT	.82	.79	-	-.0381	.744	.410
LP	.14	.47	-.17	-	.768	-.0613
OPAC	-.02	.15	.05	.16	-	-13.82
KHM	.39	.20	.36	-.17	-.15	-

Table 10. Estimates of phenotypic variances and heritabilities on an individual S_0 plant basis

Trait	Phenotypic variance	Heritability
HIST	0.00110	0.22
LYS	0.00201	0.28
PROT	0.9474	0.31
LP	0.1030	0.35
OPAC	380.6	0.08

was 23.45 $\pm$ 1.38. With the latter value as phenotypic variance and the estimate of additive genetic variance from the design II experiment, a single-plant heritability of 0.16 was calculated.

The relative efficiency for seventeen traits in selection for YLD, LYS, LP, and KH in S_1, full-sib, and S_2 recurrent selection was calculated as an aid in determining which traits would be most valuable in a selection index (Table 11). Relative efficiencies were influenced very little by the choice of recurrent selection scheme. All relative efficiencies for indirect selection were less than 1.00, indicating that no single trait could substitute for YLD, KH, LYS, or LP without some decline in genetic gain. SPGRAV, HP, and KFRACT had low efficiencies for improving all traits.

Further evidence concerning the relative value of traits and the effects of correlations on attempts to improve opaque-2 maize came from predicted gains from direct selection (Table 12). Direct selection for YLD was expected to have adverse effects on PROT, LYS, and KH. Selection for KWT produced a favorable response in YLD and KH, but decreased PROT, LYS, and LP. Selection for any of the three traits SPGRAV, KH, and TWT produced increases in the other two traits and PROT, but decreased YLD, MOIST, and LP. SPGRAV had less effect than KH and TWT, probably because of its lower

Table 11. Relative efficiencies of seventeen traits in indirect selection to improve YLD, LYS, LP, and KH in three recurrent selection schemes, S_1 testing, full-sib testing, and S_2 testing

	Selection Scheme											
	S_1				Full-sib				S_2			
Trait improved	YLD	KH	LYS	LP	YLD	KH	LYS	LP	YLD	KH	LYS	LP
Trait selected												
YLD	-	.31	.24	.01	-	.30	.24	.01	-	.32	.25	.01
MOIST	.25	.54	.08	.33	.27	.57	.08	.37	.23	.51	.08	.31
KWT	.51	.20	.29	.20	.57	.21	.31	.23	.47	.19	.28	.19
SPGRAV	.11	.18	.31	.37	.10	.16	.28	.34	.12	.19	.34	.39
ER	.49	.37	.33	.02	.50	.37	.33	.02	.47	.37	.33	.02
KH	.37	-	.10	.69	.38	-	.10	.72	.37	-	.11	.68
PROT	.41	.60	.84	.34	.43	.61	.86	.36	.39	.58	.83	.32
LYS	.32	.12	-	.40	.33	.12	-	.42	.31	.11	-	.39
LP	.01	.65	.34	-	.01	.62	.32	-	.01	.66	.35	-
HIST	.52	.51	.84	.14	.54	.52	.86	.15	.50	.50	.83	.13
HP	.27	.14	.06	.30	.26	.13	.05	.29	.28	.14	.06	.31
PYLD	.76	.02	.21	.19	.75	.02	.20	.19	.75	.02	.21	.19
LYLD	.74	.29	.36	.25	.74	.28	.34	.25	.74	.29	.36	.25
OPAC	.17	.76	.21	.67	.17	.76	.21	.70	.17	.76	.21	.66
TWT	.05	.80	.22	.65	.05	.88	.22	.70	.05	.79	.22	.63
EQUAL	.44	.43	.35	.45	.45	.43	.34	.46	.44	.44	.35	.45
KFRACT	.30	.19	.00	.38	.29	.18	.00	.38	.30	.19	.00	.38

Table 12. Expected gains per cycle from direct selection for seventeen traits by S_1 recurrent selection with testing at two locations with two replications per location and a selection intensity of 20%

Trait selected	Direction of selection	Expected Gain in Trait						
		YLD	MOIST	KWT	SPGRAV	ER	KH	PROT
YLD	+	6.00	-0.53	3.01	-0.002	-0.20	-0.65	-0.18
MOIST	-	1.49	-3.61	-1.14	-.003	.09	-1.12	-.21
KWT	+	3.01	.40	10.74	.001	.07	.42	-.10
SPGRAV	+	-.69	.29	.36	.014	.01	.36	-.04
ER	-	2.92	.49	-1.09	.000	-.57	.76	.19
KH	+	-2.25	1.37	1.43	.005	-.18	2.08	.31
PROT	+	-2.40	1.00	-1.37	-.002	-.18	1.23	.67
LYS	+	-1.95	.21	-2.31	-.009	-.18	.23	.49
LP	+	-.08	-.78	-1.34	-.009	-.01	-1.36	-.16
HIST	+	-3.15	1.18	-1.16	-.007	-.06	1.05	.59
HP	-	1.62	-.76	.05	.008	-.11	.28	.07
PYLD	+	4.54	.03	2.07	-.004	-.27	-.04	.19
LYLD	+	4.47	-.41	1.46	-.008	-.29	-.58	.13
OPAC	-	-1.00	.28	-3.77	.014	-.07	1.57	.11
TWT	+	-.30	.51	-.48	.016	-.09	1.68	.11
KQUAL	-	2.62	.68	5.68	.004	-.08	.90	-.04
KFRACT	-	1.78	.51	-1.87	.000	-.39	.40	.13
Population mean		64.8	23.0	77.9	1.13	1.87	61.1	8.68
Std. dev.[a]		8.5	3.0	8.5	.03	.57	2.5	.62

[a]Phenotypic standard deviation (S_1 family basis).

Expected Gain in Trait									
LYS	LP	HIST	HP	PYLD	LYLD	OPAC	TWT	KQUAL	KFRACT
-0.007	.00	-.007	-.03	42.5	1.76	.78	-.06	-.12	-.06
-.002	.06	-.007	-.04	-.8	.46	.61	-.28	.09	.05
-.008	-.04	-.002	.00	19.4	.57	2.91	-.09	-.25	.07
-.009	-.08	-.004	-.04	-11.0	-.91	-2.94	.88	-.05	.00
.009	.00	.002	-.03	37.8	1.68	-.86	.28	-.05	-.21
.003	-.14	.008	-.01	-1.4	-.79	-4.17	1.14	-.14	-.05
.023	-.07	.017	-.02	24.7	.67	-1.15	.29	.03	-.06
.027	.08	.014	.01	15.0	1.13	1.30	-.34	.13	.00
.009	.20	-.002	.03	-11.5	.65	3.46	-.86	.14	.09
.023	-.03	.019	.06	13.5	.42	-.58	-.16	.11	.05
-.001	-.06	-.008	-.09	-18.1	.46	-1.01	.70	-.14	-.15
.005	-.04	.003	-.03	54.7	2.10	.15	.19	-.10	-.09
.010	.05	.002	-.02	50.0	2.38	1.56	-.33	-.04	-.05
-.006	-.13	.002	-.02	-1.8	-.79	-6.67	1.40	.03	-.09
-.006	-.13	-.002	-.06	8.9	-.66	-5.51	1.86	-.16	-.13
-.009	-.09	-.005	-.05	19.7	.34	.47	.68	-.30	-.03
.000	-.08	-.003	-.07	23.2	.51	-1.96	.69	-.03	-.21
.376	4.35	.237	2.74	590.3	25.63	91.5	55.5	2.92	1.94
.029	.25	.018	.14	79.9	3.35	6.6	1.68	.39	.31

heritability. The favorable association of ER with most other traits was evident in expected increases in YLD, KH, PROT, LYS, and TWT from selection for ER. Selecting for PROT or HIST increased KH but decreased YLD, KWT, and LP; selection for LYS had a similar detrimental effect on YLD and KWT. Substantial increases in YLD were expected from selection for PYLD and LYLD, but effects on KH were adverse. Selecting for modified endosperm (low OPAC) had a beneficial effect on KH, SPGRAV, and TWT, but decreased KWT and YLD. The correlated responses to selection for KQUAL were similar to those for KWT.

As a further means of examining the value of traits, all possible three-trait selection indices having YLD as one trait were calculated (Table 13). The importance of ER was apparent in the results; all but one of the yield increases greater than 3.0 q/ha came from indices that included ER.

Based on these evaluations, eleven of the seventeen traits (YLD, MOIST, KWT, ER, KH, PROT, LYS, LP, HIST, OPAC, KQUAL) were retained for consideration in further indices. SPGRAV, HP, TWT, and KFRACT were eliminated because of low heritabilities or lack of useful correlations with more important traits; PYLD and LYLD were considered redundant in the presence of YLD, PROT, and LYS.

Table 13. Expected gain per cycle in YLD from the application of restricted[a] indices with YLD and two other traits in S_1 recurrent selection with testing at two locations, two replications per location, and a 20% selection intensity

Trait 1	Trait 2														
	MOIST	KWT	SPGRAV	ER	KH	PROT	LYS	LP	HIST	HP	PYLD	LYLD	OPAC	TWT	KQUAL
KWT	0.54														
SPGRAV	1.87	2.04													
ER	3.74	3.08	4.02												
KH	0.32	0.80	2.11	3.78											
PROT	0.02	0.50	1.75	3.81	0.32										
LYS	2.55	2.91	1.10	3.94	2.69	2.02									
LP	1.84	1.85	0.88	3.92	2.80	1.86	2.16								
HIST	0.89	0.31	1.80	3.37	1.13	1.37	1.95	1.75							
HP	1.02	1.31	0.78	3.82	1.09	1.19	1.63	0.18	1.27						
PYLD	0.26	0.63	1.45	3.80	0.05	0.57	1.82	1.33	1.44	0.91					
LYLD	2.23	2.51	0.50	3.87	2.38	1.75	1.63	1.56	1.84	1.16	1.48				
OPAC	0.76	1.00	1.91	3.81	0.99	0.74	2.73	2.25	1.26	0.72	0.37	2.31			
TWT	0.40	0.83	2.40	3.75	0.23	0.38	2.92	2.76	1.05	1.08	0.05	2.56	0.94		
KQUAL	0.23	0.86	2.02	3.60	0.06	0.18	3.01	2.21	0.91	1.10	0.08	2.57	0.62	0.22	
KFRACT	1.17	1.29	0.90	4.10	1.20	1.17	1.80	0.31	1.41	0.08	0.86	1.32	0.75	1.17	1.12

[a]Restrictions were that gains in YLD, KH and LP be in the ratio 200:24:1. No restrictions on MOIST or PROT were imposed.

Indices for S_1 Testing

In a preliminary examination of selection indices for S_1 recurrent selection, 120 four-trait combinations (incorporating YLD and three of the remaining ten traits) were used in the calculation of restricted selection indices (Tables 14, 15, and 16).

In this and subsequent comparisons of indices incorporating various combinations of traits, combinations were divided into four types as follows:

I) combinations including ER;

II) combinations excluding ER and including more than one of the traits PROT, LYS, LP, and HIST;

III) combinations excluding ER and including only one of the traits PROT, LYS, LP, and HIST;

IV) combinations excluding ER, PROT, LYS, LP, and HIST.

Type I combinations were distinguished from the other types because indices that included ER produced higher expected gains than did the other types and because type I indices placed a heavy weight on ER, consistent with the high heritability and favorable correlations estimated for the character. However, the expression of ER is dependent upon environment: in some seasons selection for ER may be impossible because of environmental conditions that do not favor disease development. In effect, this implies that the heritability of ER is environment-dependent. Further,

in other experiments involving opaque-2 maize, correlations of ER with YLD, LYS, and LP have been quite different from those reported in this experiment (Gulya, 1978; P. J. Loesch,[1] unpublished data). The usefulness of a type I index would therefore be limited.

Type II and III indices were distinguished based on expected gain and the nature of the weights specified by the index. Type II indices were frequently superior to type III indices in expected gain. However, when more than one of the traits PROT, LYS, LP, and HIST were included in an index, the weights shifted to place considerable selection pressure on a linear combination of the protein-related traits, generally in antagonistic fashion. Index 14-53 (YLD + 3.3 KWT + 450 LYS - 521 HIST; Table 15) provides an instructive example. The importance of 450 LYS - 521 HIST relative to YLD is given by

$$R = \frac{s_{P;YLD}}{\sqrt{(450)^2 s^2_{P;LYS} + (521)^2 s^2_{P;HIST} - 2(450)(521) s_{P;LYS,HIST}}} = 0.93.$$

Thus, the two terms appear to have roughly equal roles in selection. However, the determination of relative importance is highly dependent on reliable estimates of the relevant variances and covariances. Because significant

[1] Science and Education Administration, U.S. Department of Agriculture and Department of Agronomy, Iowa State University, Ames, Iowa.

Table 14. Expected gain per cycle in YLD for 120 four-trait restricted[a] selection indices in S_1 recurrent selection with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
14-1	I		X	X	X	X								4.04
14-2	I	M	X	X		X	X							3.78
14-3	I	M	X	X		X		X						3.81
14-4	I	M	X	X		X			X					3.89
14-5	I	M	X	X		X				X				3.85
14-6	I		X	X		X					X			3.74
14-7	I	M	X	X		X						X		3.80
14-8	I		X	X		X							X	3.74
14-9	I	M	X		X	X	X							1.67
14-10	I	M	X		X	X		X						.95
14-11	I	M	X		X	X			X					1.45
14-12	I	M	X		X	X				X				1.61
14-13	I	M[b]	X		X	X					X			3.14
14-14	I	M	X		X	X						X		2.20
14-15	I	M	X		X	X							X	1.39
14-16	I	M[b]	X			X	X	X						2.22
14-17	I	M	X			X	X		X					.34
14-18	I	M	X			X	X			X				.14
14-19	I	M[b]	X			X	X				X			3.12
14-20	I	M	X			X	X					X		3.37
14-21	I	M	X			X	X						X	1.61
14-22	I	M[b]	X			X		X	X					1.05
14-23	I	M[b]	X			X		X		X				2.03
14-24	I	M[b]	X			X		X			X			3.12
14-25	I	M[b]	X			X		X				X		3.28
14-26	I	M[b]	X			X		X					X	.54
14-27	I	M	X			X			X	X				.56
14-28	I	M[b]	X			X			X		X			2.95
14-29	I	M	X			X			X			X		3.36

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

[b]Negative gain in PROT obtained; M and P restrictions could not be applied simultaneously (see text).

Table 14 (Continued)

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
14-30	I	M[b]	X			X			X				X	.97
14-31	I	M[b]	X			X				X	X			3.06
14-32	I	M	X			X				X		X		3.97
14-33	I	M[b]	X			X				X			X	1.56
14-34	I	M[b]	X			X					X	X		3.17
14-35	I	M[b]	X			X					X		X	3.08
14-36	I	M	X			X						X	X	2.87
14-37	II	M	X	X				X	X					1.90
14-38	II	M	X	X				X		X				1.71
14-39	II	M	X	X				X			X			1.25
14-40	II	M	X	X					X	X				2.10
14-41	II	M	X	X					X		X			1.69
14-42	II	M	X	X						X	X			1.50
14-43	II	M	X		X			X	X					.38
14-44	II	M[b]	X		X			X		X				.12
14-45	II	M[b]	X		X			X			X			.25
14-46	II	M[b]	X		X				X	X				1.33
14-47	II	M[b]	X		X				X		X			1.31
14-48	II	M[b]	X		X					X	X			.65
14-49	II	M[b]	X				X	X	X					2.79
14-50	II	M[b]	X				X	X		X				1.63
14-51	II	M[b]	X				X	X			X			.15
14-52	II	M	X				X		X	X				.68
14-53	II		X				X		X		X			3.05
14-54	II	M[b]	X				X			X	X			2.51
14-55[c]	II		X					X	X	X				3.34
14-56	II	M	X					X	X		X			1.88
14-57	II		X					X	X			X		3.00
14-58	II	M[b]	X					X	X				X	.32
14-59	II	M	X					X		X	X			1.51
14-60	II		X					X		X		X		2.76
14-61	II	M[b]	X					X		X			X	.12
14-62	II	M[b]	X					X			X	X		.51
14-63	II	M	X					X			X		X	.08
14-64	II		X						X	X	X			2.18
14-65	II		X						X	X		X		2.90
14-66	II	M	X						X	X			X	1.26
14-67	II		X						X		X	X		2.96

[c]Index calculated using nonpositive-definite genetic variance-covariance matrix (see text).

Table 14 (Continued)

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
14-68	II	M	X						X		X		X	2.68
14-69	II		X							X	X	X		2.60
14-70	II	M[b]	X							X	X		X	.97
14-71	III	P	X	X	X			X						.48
14-72	III	M[b]	X	X	X				X					2.65
14-73	III	M[b]	X	X	X					X				1.66
14-74	III		X	X	X						X			1.03
14-75	III	M	X	X			X	X						.30
14-76	III	M	X	X			X		X					2.65
14-77	III	M	X	X			X			X				2.74
14-78	III	M	X	X			X				X			1.08
14-79	III	M	X	X				X				X		.63
14-80	III	M	X	X				X					X	.18
14-81	III	M	X	X					X			X		2.76
14-82	III	M[b]	X	X					X				X	2.94
14-83	III	M[b]	X	X						X		X		2.50
14-84	III	M[b]	X	X						X			X	2.04
14-85	III	M	X	X							X	X		1.15
14-86	III		X	X							X		X	.94
14-87	III	M[b]	X		X		X	X						.24
14-88	III	M	X		X		X		X					1.53
14-89	III	M[b]	X		X		X			X				1.44
14-90	III	M[b]	X		X		X				X			.24
14-91	III	M[b]	X		X			X				X		.33
14-92	III	M[b]	X		X			X					X	.03
14-93	III	M	X		X				X			X		3.18
14-94	III	M	X		X				X				X	.89
14-95	III	P[b]	X		X					X		X		.22
14-96	III	M[b]	X		X					X			X	.34
14-97	III	M[b]	X		X						X	X		.14
14-98	III	M[b]	X		X						X		X	.38
14-99	III	M	X				X	X				X		.06
14-100	III	M	X				X	X					X	.13
14-101	III		X				X		X			X		2.76
14-102	III	M[b]	X				X		X				X	1.42
14-103	III	M[b]	X				X			X		X		2.95
14-104	III	M	X				X			X			X	1.30
14-105	III	M	X				X				X	X		.46
14-106	III	M	X				X				X		X	.23
14-107	III	M	X					X				X	X	.13

Table 14 (Continued)

Index no.	Type	Restrictions[a]	YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	Gain in YLD (q/ha)
14-108	III	M	X						X			X	X	2.98
14-109	III	P	X							X		X	X	.11
14-110	III	M_b	X								X	X	X	.36
14-111	IV	M_b	X	X	X		X							.78
14-112	IV	M_b	X	X	X							X		.92
14-113	IV	M_b	X	X	X								X	.85
14-114	IV	M_b	X	X			X					X		.87
14-115	IV	M_b	X	X			X						X	.05
14-116	IV	M_b	X	X								X	X	.50
14-117	IV	M_b	X		X		X					X		.52
14-118	IV	M_b	X		X		X						X	.47
14-119	IV	M_b	X		X							X	X	.66
14-120	IV	M	X				X					X	X	.12

deviations from predicted correlated responses have been frequently reported, especially under conditions of antagonistic selection (Clayton et al., 1957a; Bohren et al., 1966; Rutledge et al., 1973; Moll et al., 1975), use of a type II index would entail a risk of producing unsatisfactory genetic changes in the population. By comparison, type III indices appeared to make greater use of direct responses and to be less dependent on correlations.

Use of type IV indices would not require chemical evaluation for protein traits and thus would be relatively inexpensive. Expected gains from such indices (Table 14), however, were very low. A few type I indices produced

Table 15. Weights of indices from Table 14 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD (q/ha)	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
14-1	I		4.04	-1	-11.5	3.28	-136							
14-32	I	M	3.99	1			-29				32.2		-1.4	
14-4	I	M	3.89	1	-1.3		-63			150				
14-5	I	M	3.85	1	-1.8		-95				9.3			
14-3	I	M	3.81	1	-3.4		-200		-22.7					
14-7	I	M	3.80	1	-2.6		-121						.6	
14-2	I	M	3.78	1	-2.6		-140	-1.9						
14-6	I		3.74	1	-6.1		-138					124		
14-8	I		3.74	1	-11.2		-228							-11.0
14-53	II		3.05	1				3.3		450		-521		
14-57	II		3.00	1					-8.3	402			-1.3	
14-67	II		2.96	1						482		-351	-1.3	
14-65	II		2.90	1						230	12.7		-1.2	
14-93	III	M	3.18	1		.35				357			-.6	
14-108	III	M	2.98	1						349			-.5	-5.3
14-82	III	M	2.94	1	-.6					527				-30.6
14-81	III	M	2.76	1	.1					312			-.6	
14-101	III		2.76	1				.5		299			-.4	
14-77	III	M	2.74	1	-.3			3.9			28.5			
14-72	III	M	2.65	1	-3.3	9.15				1506				
14-76	III	M	2.65	1	-.2			1.5		272				
14-114	IV	M	.87	1	-2.5			11.8					4.2	
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				8.5	3.0	8.5	.57	2.5	.62	.029	.25	.018	6.6	.39

[a]See Table 14 for description of restrictions.

[b]Phenotypic standard deviation (S_1 family basis).

satisfactory expected gains without protein data.

Many of the four-trait indices required restrictions on MOIST because of expected increases in MOIST when the restriction was omitted. Applying such a restriction to an index that did not include MOIST as a trait generally resulted in a substantially lower gain in YLD. For example, the index YLD + 1.032 KWT + 0.984 KH + 405 LYS was expected to produce increases of 3.17 q/ha in YLD and 0.31% in MOIST. With the application of a restriction on MOIST, the index became YLD - 0.623 KWT + 1.623 KH + 188 LYS (index 14-88, Table 14) and the expected gain was 1.52 q/ha for YLD (and 0.0 for MOIST). Since MOIST was not included in the index, the requirement of zero expected gain in MOIST had to be met through correlated responses involving a combination of the other traits, which severely limited the potential for progress in YLD. By contrast, the index YLD + 0.739 MOIST + 0.903 KH + 261 LYS, which produced gains of 2.75 q/ha in YLD and 0.81% in MOIST, could be restricted (YLD - .212 MOIST + 1.52 KH + 272 LYS; index 14-76, Table 14) to hold MOIST constant while allowing a gain of 2.65 q/ha in YLD. The presence of OPAC in an index that did not include MOIST appeared to reduce the detrimental effect on YLD of introducing a restriction on MOIST (e.g., indices 14-20, 14-93, Table 14).

A few combinations of traits required restrictions on PROT; some required both MOIST and PROT restrictions, but it was impossible to apply both since only n-1 restrictions were possible with an index of n traits (James, 1968) and two restrictions (on gain in KH and LP) were applied to every index, permitting only one additional restriction.

The index that was expected to produce the greatest gain in YLD (index 14-1) actually had a negative weight for YLD (Table 15). The large weights on MOIST, KWT, and ER were expected to produce a large correlated response in YLD. In other type I indices listed in Table 15, the importance of ER relative to YLD ranged from 2 to 15, indicating reliance on increased resistance to ear rot to improve productivity.

Of the combinations of traits examined, one, represented by index 14-55 (Table 14), had to be eliminated from consideration because of a nonpositive-definite genetic variance-covariance matrix. This index, which exceeded all other type II indices in expected gain in YLD, had weights that gave YLD very little importance relative to the other traits: YLD - 287 PROT + 7027 LYS - 553 LP. The available estimates for genetic variances and covariances of component traits yielded a negative estimate (-62170.8) for the genetic variance of this index. Thus, the calculated expected gain for this index was meaningless.

The weights of most type III indices were such that

the importance relative to YLD of most component traits was not excessive, although the relative importance of LYS generally exceeded 1.0. Index 14-72, with its large weights on KWT and LYS, was an exception.

Since the restrictions employed in calculating these indices imposed gains in KH and LP, it is somewhat surprising that these two traits appeared in few of the most effective indices (Table 15). The presence of LYS and OPAC in several indices was expected to give correlated responses in KH and LP. Perhaps limiting an index to four traits caused preferential inclusion of those traits whose correlations would make them effective selectors for more than one of the characters in which improvement was required.

The strong association between KWT and KQUAL was reflected in the fact that the two traits could substitute for one another with little change in effectiveness (compare 14-1 and 14-8, 14-93 and 14-108, and 14-72 and 14-82, Table 15).

The expected gains per cycle in all traits from the application of the most effective four-trait indices are given in Table 16. Gains in KH and LP were, respectively, 0.12 and 0.005 times the gain in YLD, as required by the restrictions. Consequently, gains in KH and LYS, like those in YLD, were highest with type I indices. All indices changed PROT, LYS, and ER in the desired direction.

Table 16. Expected gains per cycle from four-trait indices listed in Table 15

Index no.	Type	Restrictions[a]	Expected gain										
			YLD q/ha	MOIST %	KWT	ER	KH	PROT %	LYS %	LP g/100 g	HIST %	OPAC %	KQUAL
14-1	I		4.04	-.9	2.0	-.48	.49	.08	.006	.02	-.002	.4	-.09
14-32	I	M	3.99	.0	-1.7	-.53	.48	.06	.005	.02	-.001	-1.9	-.02
14-4	I	M	3.89	.0	-.7	-.57	.47	.17	.010	.02	.001	-.4	-.05
14-5	I	M	3.85	.0	-.8	-.56	.46	.13	.008	.02	.000	-.5	-.06
14-3	I	M	3.81	.0	-.8	-.55	.46	.08	.006	.02	-.001	-.6	-.06
14-7	I	M	3.80	.0	-.6	-.56	.46	.14	.008	.02	.000	-.3	-.06
14-2	I	M	3.78	.0	-.9	-.56	.45	.13	.008	.02	.000	-.5	-.05
14-6	I		3.74	-.4	-1.0	-.55	.45	.14	.008	.02	.000	-.6	-.04
14-8	I		3.74	-.5	-1.0	-.55	.45	.12	.008	.02	-.001	-.6	-.05
14-53	II		3.05	-.1	1.5	-.40	.37	.16	.009	.02	.001	-.4	-.13
14-57	II		3.00	-.5	-2.4	-.32	.36	.16	.009	.01	.003	-2.6	.05
14-67	II		2.96	-.6	-2.6	-.37	.35	.22	.011	.01	.003	-2.3	.02
14-65	II		2.90	-.3	-2.2	-.33	.35	.20	.011	.01	.004	-2.4	.05
14-93	III	M	3.18	.0	1.7	-.32	.38	.33	.016	.02	.008	.2	-.03
14-108	III	M	2.98	.0	.0	-.35	.36	.34	.016	.01	.007	-.2	-.03
14-82	III	M	2.94	.0	2.8	-.27	.35	.27	.013	.01	.004	1.8	-.14
14-81	III	M	2.76	.0	-1.0	-.35	.33	.34	.016	.01	.008	-.9	.02
14-101	III		2.76	.0	-.3	-.35	.33	.34	.016	.01	.008	-.5	.00
14-77	III	M	2.74	.0	2.6	-.30	.33	.01	.003	.01	.000	-.7	-.12
14-72	III	M	2.65	.0	9.2	-.03	.32	.12	.006	.01	.004	3.6	-.17
14-76	III	M	2.65	.0	1.1	-.34	.32	.32	.016	.01	.008	.2	-.05
14-114	IV	M	.87	.0	5.7	-.14	.10	.10	.006	.00	.002	2.6	-.18

[a]See Table 14 for description of restrictions.

Compared to types I and II, type III indices tended to give greater advance in PROT, LYS, and HIST. Type III indices increased KWT and, in four cases out of eight, increased OPAC, while type I and II indices generally decreased KWT and OPAC.

Based on results with the four-trait indices, 110 combinations of five traits were chosen for index calculation (Tables 17, 18, and 19). These combinations, which represented approximately half of the total possible combinations incorporating YLD and four other traits, were obtained by augmenting the more effective four-trait indices of each type.

The best five-trait indices produced considerably higher expected gains than the best four-trait indices (Table 19). Adding MOIST to four-trait combinations lacking that character generally made addition of a restriction on gain in MOIST possible without a significant reduction of YLD gains. High YLD gains from an index carrying a restriction on PROT were possible if PROT or a highly correlated trait such as KH, LYS, or HIST was present, but not if LP was the sole measure of protein quality and KH was absent (e.g., indices 17-91 and 17-92, Table 17).

Type IV indices had very low expected gains.

Nonpositive-definite matrices were obtained with eight combinations (Table 17). Five of these included the three

Table 17. Expected gain per cycle in YLD for 110 five-trait restricted[a] selection indices in S_1 recurrent selection with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
17-1	I	M	X	X	X	X	X							4.33
17-2	I	P	X	X	X	X		X						4.21
17-3	I		X	X	X	X			X					4.52
17-4	I	M	X	X	X	X				X				4.55
17-5	I		X	X	X	X						X		4.23
17-6	I		X	X	X	X							X	4.15
17-7	I	M	X	X		X	X	X						3.81
17-8	I	M	X	X		X	X		X					3.93
17-9	I	M	X	X		X	X			X				4.03
17-10	I	M	X	X		X	X					X		3.81
17-11	I	M	X	X		X	X						X	3.88
17-12	I	M	X	X		X		X	X					3.89
17-13	I	M	X	X		X		X		X				3.86
17-14	I	M	X	X		X		X				X		3.81
17-15	I		X	X		X		X					X	3.86
17-16	I	M	X	X		X			X	X				3.89
17-17	I	M	X	X		X			X		X			3.89
17-18	I	M	X	X		X			X			X		3.93
17-19	I		X	X		X			X				X	4.13
17-20	I	M	X	X		X				X	X			3.88
17-21	I	M	X	X		X				X		X		4.01
17-22	I	M	X	X		X				X			X	4.27
17-23	I	M	X		X	X			X			X		3.37
17-24	I	MP	X		X	X				X		X		4.64
17-25	I	M	X			X	X		X		X			3.97
17-26	I	M	X			X	X		X			X		3.80
17-27	I	MP	X			X	X			X	X			1.97
17-28	I	M	X			X	X			X		X		4.01
17-29	I	M	X			X		X	X			X		4.13
17-30	I	M	X			X		X		X		X		3.99
17-31	I	M	X			X			X	X		X		4.02
17-32	I	M	X			X			X		X	X		4.02
17-33	I	M	X			X			X			X	X	3.44
17-34	I	M	X			X				X	X	X		3.99
17-35	I	MP	X			X				X		X	X	4.32
17-36	II	M	X	X	X			X	X					2.80

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

Table 17 (Continued)

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
17-37	II	M	X	X	X			X		X				2.57
17-38	II	M	X	X	X				X	X				2.88
17-39	II	M	X	X	X				X		X			2.71
17-40	II	M	X	X			X	X	X					3.05
17-41	II	M	X	X			X	X		X				2.78
17-42	II	M	X	X			X		X	X				2.87
17-43	II	M	X	X			X		X		X			3.11
17-44	II	M	X	X			X			X	X			2.74
17-45	II	M	X	X				X	X			X		3.17
17-46	II	M	X	X				X	X				X	3.02
17-47	II	M	X	X				X		X		X		2.86
17-48	II	M	X	X				X		X			X	2.71
17-49	II	M	X	X					X	X		X		3.01
17-50	II	M	X	X					X	X			X	2.97
17-51	II	M	X	X					X		X	X		3.19
17-52	II	M	X	X					X		X		X	3.03
17-53	II	M	X	X						X	X	X		2.68
17-54	II	M	X	X						X	X		X	2.55
17-55	II	MP	X	X						X		X	X	.70
17-56	II	MP	X		X		X	X	X					2.71
17-57[b]	II	M	X		X		X		X		X			3.55
17-58[b]	II		X		X			X	X	X				3.94
17-59	II		X		X			X	X			X		4.20
17-60	II		X		X			X		X		X		3.97
17-61	II		X		X				X	X		X		4.07
17-62	II		X		X				X		X	X		4.27
17-63[b]	II	MP	X		X				X		X		X	2.68
17-64[b]	II	P	X				X	X	X	X				3.74
17-65	II		X				X	X	X		X			3.16
17-66	II		X				X	X	X			X		3.27
17-67	II	MP	X				X	X	X				X	2.58
17-68	II	M	X				X	X		X	X			2.81
17-69	II		X				X	X		X		X		3.04
17-70	II		X				X		X	X	X			3.08
17-71	II		X				X		X	X		X		3.11
17-72	II		X				X		X		X	X		3.19
17-73[b]	II		X				X		X		X		X	3.42
17-74[b]	II		X					X	X	X	X			3.34
17-75[b]	II		X					X	X	X		X		3.54
17-76[b]	II		X					X	X	X			X	3.98

[b]Index calculated using nonpositive-definite genetic variance-covariance matrix.

Table 17 (Continued)

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
17-77	II		X					X	X		X	X		3.02
17-78	II	M	X					X	X		X		X	2.88
17-79	II		X					X	X			X	X	3.87
17-80	II		X					X		X	X	X		2.77
17-81	II		X					X		X		X	X	3.61
17-82	II		X						X	X	X	X		2.97
17-83	II	M	X						X	X	X		X	3.05
17-84	II		X						X	X		X	X	3.71
17-85	II		X						X		X	X	X	3.65
17-86	III	M	X	X	X		X	X						.92
17-87	III	M	X	X	X		X		X					3.11
17-88	III	MP	X	X	X		X			X				2.86
17-89	III	M	X	X	X				X			X		3.39
17-90	III	M	X	X	X				X				X	3.18
17-91	III	MP	X	X	X					X		X		.73
17-92	III	MP	X	X	X					X			X	.22
17-93	III	M	X	X			X		X			X		2.76
17-94	III	M	X	X			X		X				X	2.99
17-95	III	MP	X	X			X			X		X		2.84
17-96	III	MP	X	X			X			X			X	2.86
17-97[b]	III	M	X	X					X			X	X	3.08
17-98[b]	III		X		X		X		X			X		3.64
17-99	III	M	X		X		X		X				X	1.56
17-100	III	MP	X		X		X			X		X		2.70
17-101[b]	III	M	X		X		X			X			X	1.46
17-102[b]	III	M	X		X				X			X	X	3.23
17-103[b]	III	MP	X		X					X		X	X	.19
17-104[b]	III	M	X				X		X			X	X	3.15
17-105	III	MP	X				X			X		X	X	2.72
17-106	IV	M	X	X	X		X					X		1.05
17-107	IV	MP	X	X	X		X						X	.71
17-108	IV	MP	X	X	X							X	X	.19
17-109	IV	M	X	X			X					X	X	.89
17-110	IV	MP	X		X		X					X	X	.60

traits PROT, LYS, and LP, while the other three were of type III.

Weights for the most effective indices of each class (Table 18) were similar to those for four-trait indices (Table 15). Index 17-4 had a negative weight for YLD and very high weights for MOIST, KWT, ER, and LP; the aberrant set of weights was because of the restriction on MOIST, since the unrestricted index was YLD - .69 MOIST + 7.8 KWT - 185 ER + 94.6 LP. Index 17-1 also had a negative weight for YLD. The importance of KWT and OPAC relative to YLD was often greater than 1 for type I and II indices, while the relative importance of YLD in type III indices was fairly high with the exception of 17-90, in which weights for MOIST, KWT, LYS, and KQUAL were all greater than those of other type III indices. The most effective indices of type III included LYS rather than LP as the measure of protein quality. Generally, KWT was more useful than KQUAL (compare 17-89 and 17-97, 17-87 and 17-94). KWT and MOIST were required for maximum advance.

Expected gains for the most effective indices are shown in Table 19. Superiority of types of indices with respect to expected gain in YLD was in the order I > II > III, and the difference between types II and III was more pronounced with the five-trait indices than with the four-trait indices (Table 16).

Table 18. Weights of five-trait indices from Table 17 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD q/ha	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
17-24	I	MP	4.64	1		.93	-27				49.7		-2.0	
17-4	I	M	4.55	-1	-222	288	-6962				2634			
17-3	I		4.52	1	-2.5	2.57	-58			511				
17-1	I	M	4.33	-1	-2.7	3.45	-100	-4.5						
17-35	I	MP	4.32	1			-24				50.6		-1.8	-17
17-22	I	M	4.27	1	-5.0		-165				106.4			-127
17-62	II		4.27	1		2.05				1118		-1189	-2.4	
17-59	II		4.20	1		1.43			-21	702			-1.9	
17-61	II		4.07	1		1.28				246	-32.6		-1.7	
17-60	II		3.97	1		1.32			10		54.2		-1.8	
17-79	II		3.87	1					-20	675			-1.4	-25
17-89	III	M	3.39	1	-.2	.98				439			-.6	
17-90	III	M	3.18	1	-1.0	1.25				661				-26
17-87	III	M	3.11	1	-.6	1.05		1.3		414				
17-97	III	M	3.08	1	-.2					410			-.3	-14
17-94	III	M	2.99	1	-.5			.6		428				-19
17-88	III	MP	2.86	1	-.3	.14		4.0			30.6			
17-96	III	MP	2.86	1	-.3			3.9			31.0			-2.8
17-95	III	MP	2.84	1	-.2			3.5			29.8		-.2	
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				8.5	3.0	8.5	.57	2.5	.62	.029	.25	.018	6.6	.39

[a] See Table 17 for description of restrictions.

[b] Phenotypic standard deviation (S_1 family basis).

Table 19. Expected gains per cycle from five-trait indices listed in Table 18

Index no.	Type	Restrictions[a]	Expected Gain										
			YLD q/ha	MOIST %	KWT	ER	KH	PROT %	LYS %	LP g/100 g	HIST %	OPAC %	KQUAL
17-24	I	MP	4.64	.0	1.2	-.48	.56	.00	.003	.02	-.002	-1.2	-.07
17-4	I	M	4.55	.0	4.7	-.46	.55	.06	.005	.02	-.001	1.5	-.15
17-3	I		4.52	-.1	4.2	-.48	.54	.19	.011	.02	.002	1.5	-.13
17-1	I	M	4.33	.0	3.7	-.46	.52	.08	.005	.02	-.001	1.5	-.13
17-35	I	MP	4.32	.0	-.6	-.49	.52	.00	.003	.02	-.003	-1.6	-.08
17-22	I	M	4.27	.0	1.2	-.52	.51	.06	.005	.02	-.003	.5	-.15
17-62	II		4.27	-.5	4.8	-.28	.51	.08	.005	.02	-.001	.4	-.15
17-59	II		4.20	-.3	5.0	-.20	.50	.02	.003	.02	.001	.0	-.09
17-61	II		4.07	-.1	5.1	-.21	.49	.06	.004	.02	.001	.1	-.09
17-60	II		3.97	-.1	5.2	-.21	.48	.04	.004	.02	.001	.0	-.10
17-79	II		3.87	-.2	.9	-.29	.46	.03	.003	.02	-.002	-.7	-.11
17-89	III	M	3.39	.0	4.9	-.25	.41	.29	.014	.02	.007	1.6	-.09
17-90	III	M	3.18	.0	6.1	-.20	.38	.24	.011	.02	.005	2.9	-.17
17-87	III	M	3.11	.0	6.1	-.22	.37	.26	.013	.02	.007	2.2	-.13
17-97	III	M	3.08	.0	1.4	-.33	.37	.32	.015	.02	.006	.8	-.08
17-94	III	M	2.99	.0	2.4	-.31	.36	.30	.014	.01	.006	1.4	-.12
17-88	III	MP	2.86	.0	3.5	-.28	.34	.00	.003	.01	-.001	-.3	-.13
17-96	III	MP	2.86	.0	2.9	-.30	.34	.00	.003	.01	-.001	-.5	-.14
17-95	III	MP	2.84	.0	2.1	-.31	.34	.00	.003	.01	-.001	-1.1	-.11

[a]See Table 17 for description of restrictions.

Forty-seven combinations of six traits were considered for index construction (Tables 20, 21, and 22). By comparison with the most effective five-trait indices of each type (Table 19), the best six-trait combinations produced relatively little additional gain, especially in type III. The most effective six-trait indices of type III (20-43 and 20-41, Table 21) differed from their five-trait counterparts (17-89 and 17-87, Table 18) only by the addition of KQUAL. Index 20-47, incorporating the maximum number of traits possible for a type IV index, had a very low expected gain; type IV indices were not considered in subsequent work. The proportion of six-trait indices rejected because of nonpositive-definite genetic variance-covariance matrices was greater than that of five-trait indices. Two type III indices having high expected gains (20-39 and 20-45) were eliminated for this reason.

Weights of six-trait indices (Table 21) were similar to those of five-trait indices. Two effective type I indices (20-12 and 20-13) conferred relatively higher importance on YLD than most type I indices.

Combinations of seven and more traits were investigated, but they were of little value. Nonpositive-definite genetic variance-covariance matrices became more frequent as the number of traits increased. The most effective seven-trait indices of types I and II produced gains in YLD of 4.96 and

Table 20. Expected gain per cycle in YLD for 47 six-trait restricted[a] selection indices in S_1 recurrent selection with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
20-1	I	M	X	X	X	X	X		X					4.56
20-2	I	M	X	X	X	X	X			X				4.59
20-3	I		X	X	X	X	X					X		4.33
20-4	I	M	X	X	X	X	X						X	4.33
20-5	I	M	X	X	X	X			X	X				4.60
20-6	I	M	X	X	X	X			X		X			4.63
20-7	I		X	X	X	X			X			X		4.52
20-8	I		X	X	X	X			X				X	4.52
20-9	I	MP	X	X	X	X				X		X		4.90
20-10	I	M	X	X	X	X				X			X	4.63
20-11	I		X	X	X	X						X	X	4.24
20-12	I	MP	X		X	X				X	X	X		4.68
20-13	I	MP	X		X	X				X		X	X	4.65
20-14	I	M	X			X	X		X			X	X	4.03
20-15	I	MP	X			X	X			X		X	X	4.33
20-16	I	MP	X			X		X		X		X	X	4.34
20-17	I	M	X			X			X	X		X	X	4.37
20-18	II	M	X	X	X			X	X			X		4.24
20-19	II	M	X	X	X				X		X	X		4.37
20-20	II		X		X		X	X	X			X		4.21
20-21	II		X		X		X	X		X		X		3.99
20-22	II		X		X		X		X		X	X		4.30
20-23	II		X		X			X	X	X	X			3.98
20-24	II	P	X		X			X	X	X		X		4.41
20-25	II		X		X			X	X	X			X	4.18
20-26	II		X		X			X	X		X	X		4.41
20-27	II	M	X		X			X	X		X		X	3.09
20-28	II	P	X		X			X	X			X	X	4.38
20-29	II		X		X			X		X	X	X		4.16
20-30	II		X		X				X	X	X	X		4.36

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

Table 20 (Continued)

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
20-31	II	M	X		X				X	X	X		X	3.34
20-32	II		X		X				X	X		X	X	4.23
20-33	II		X		X				X		X	X	X	4.34
20-34	II		X					X	X	X	X	X		3.55
20-35[b]	II		X					X	X	X	X		X	3.99
20-36[b]	II	P	X					X	X	X		X	X	4.20
20-37	II		X					X	X		X	X	X	3.92
20-38[b]	II		X						X	X	X	X	X	3.81
20-39[b]	III	M	X	X	X		X		X			X		3.66
20-40	III	MP	X	X	X		X			X		X		2.86
20-41	III	M	X	X	X		X		X				X	3.22
20-42	III	MP	X	X	X		X			X			X	2.86
20-43	III	M	X	X	X				X			X	X	3.41
20-44[b]	III	MP	X	X	X					X		X	X	.75
20-45[b]	III		X		X		X		X			X	X	3.73
20-46[b]	III	MP	X		X		X			X		X	X	2.72
20-47	IV	M	X	X	X		X					X	X	1.06

[b]Index calculated using nonpositive-definite genetic variance-covariance matrix.

4.56 q/ha, respectively, exceeding only slightly the most effective six-trait indices. Two type III combinations (YLD-MOIST-KWT-KH-LYS-OPAC-KQUAL and YLD-MOIST-KWT-KH-LP-OPAC-KQUAL) were evaluated but were rejected due to nonpositive-definite matrices. The best gains in YLD calculated for eight-trait indices of types I and II were 5.15 and 4.64 q/ha, respectively, while a type I nine-trait index produced an expected gain of 5.21 q/ha. Non-positive-definite matrices eliminated from consideration all ten-trait combinations and the index of all eleven traits.

Table 21. Weights of indices from Table 20 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD (q/ha)	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
20-9	I	MP	4.90	1	-1.0	2.93	-54				75.6		-2.4	
20-12	I	MP	4.68	1		1.00	-20				48.9	76.2	-1.9	
20-13	I	MP	4.65	1		1.10	-27				49.6		-2.0	3.07
20-6	I	M	4.63	1	-5.2	8.69	-182			1558		-1381		
20-10	I	M	4.63	-1	-53	53.4	-1512				892			-538
20-5	I	M	4.60	1	-4.6	6.02	-133			517	32.5			
20-26	II		4.41	1		1.86			-13	991		-679	-2.5	
20-28	II	P	4.38	1		1.10			-23	768			-1.8	-13.5
20-19	II	M	4.37	1	1.3	1.76				1051		-1211	-2.1	
20-30	II		4.36	1		1.87				765	19.7	-769	-2.4	
20-33	II		4.34	1		1.90				1238		-1331	-2.3	-11.5
20-43	III	M	3.41	1	-.3	.89				458			-.5	-4.4
20-41	III	M	3.22	1	-.7	.95		.65		519				-14.2
20-40	III	MP	2.86	1	-.3	.11		3.90			30.4		-.05	
20-42	III	MP	2.86	1	-.3	.06		3.97			30.8			-1.6
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				8.5	3.0	8.5	.57	2.5	.62	.029	.25	.018	6.6	.39

[a] See Table 20 for description of restrictions.

[b] Phenotypic standard deviation (S_1 family basis).

Table 22. Expected gains per cycle from six-trait indices listed in Table 21

Index no.	Type	Restrictions[a]	Expected Gain										
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
			q/ha	%	g			%	%	g/100 g	%	%	
20-9	I	MP	4.90	.0	4.1	-.45	.59	.00	.003	.02	-.002	.3	-.13
20-12	I	MP	4.68	.0	2.0	-.44	.56	.00	.003	.02	-.002	-1.0	-.08
20-13	I	MP	4.65	.0	1.5	-.47	.56	.00	.003	.02	-.002	-1.1	-.07
20-6	I	M	4.63	.0	4.8	-.47	.56	.12	.007	.02	.000	1.7	-.16
20-10	I	M	4.63	.0	4.6	-.46	.56	.04	.004	.02	-.002	1.6	-.18
20-5	I	M	4.60	.0	4.8	-.47	.55	.12	.008	.02	.001	1.6	-.15
20-26	II		4.41	-.5	4.9	-.25	.53	.01	.002	.02	-.002	-.1	-.13
20-28	II	P	4.38	-.2	4.8	-.22	.53	.00	.002	.02	-.001	.3	-.13
20-19	II	M	4.37	.0	4.8	-.31	.52	.07	.004	.02	-.001	.5	-.17
20-30	II		4.36	-.5	5.0	-.26	.52	.03	.003	.02	-.001	.0	-.14
20-33	II		4.34	-.5	4.7	-.30	.52	.08	.005	.02	-.002	.6	-.18
20-43	III	M	3.41	.0	4.9	-.25	.41	.30	.014	.02	.007	1.8	-.11
20-41	III	M	3.22	.0	5.7	-.23	.39	.26	.013	.02	.006	2.5	-.15
20-40	III	MP	2.86	.0	3.2	-.29	.34	.00	.003	.01	-.001	-.5	-.13
20-42	III	MP	2.86	.0	3.2	-.29	.34	.00	.003	.01	-.001	-.4	-.14

[a]See Table 20 for description of restrictions.

Sampling standard deviations of expected gains in YLD for several five- and six-trait indices are given in Table 23. Standard deviations were very large, approximately half the magnitude of the expected gain. Type II indices consistently had greater standard deviations than did indices of types I and III. Surprisingly, the standard deviation of the expected gain from direct selection was larger than the values for indices of types I and III. There was no apparent trend for standard deviations to change as the number of traits increased (even to seven, eight, or nine traits, for which data are not shown).

The use of restrictions on gain in the key traits KH and LP permits ranking of combinations of traits for desirability in selection indices by simply ranking them for expected gain in YLD. The particular restrictions used, however, may be expected to influence the ranking. To determine the degree to which this occurred, ten combinations of five traits were used to calculate indices in which gain in KH was restricted to 5, 12, and 25% and gain in LP to 0, 0.5, and 1% of the gain in YLD (Table 24). Indices were calculated with additional restrictions on MOIST and PROT where needed.

Although expected gains for YLD decreased substantially as restrictions on KH and LP were made more stringent, the ranks of these trait combinations were affected little. Thus,

Table 23. Sampling standard deviations of the expected gain in YLD for restricted selection indices applied to S_1 testing at two locations with the replications per location and a selection intensity of 20%

Index no.	Type	Number of traits	Expected gain in YLD (q/ha)	Standard deviation (q/ha)
17-24	I	5	4.64	1.93
17-3	I	5	4.52	1.79
17-35	I	5	4.32	1.93
20-9	I	6	4.90	1.87
20-12	I	6	4.68	1.98
20-13	I	6	4.65	1.93
20-6	I	6	4.63	1.79
20-10	I	6	4.63	1.79
17-62	II	5	4.27	2.44
17-59	II	5	4.20	2.40
17-61	II	5	4.07	2.13
20-26	II	6	4.41	2.57
20-28	II	6	4.38	2.39
20-19	II	6	4.37	2.53
20-30	II	6	4.36	2.34
20-33	II	6	4.34	2.36
17-89	III	5	3.39	1.97
17-90	III	5	3.18	1.90
17-87	III	5	3.11	1.94
20-43	III	6	3.41	1.96
20-41	III	6	3.22	1.92
Direct selection for YLD			6.00	2.13

Table 24. Effect of varying restrictions on gain in KH and LYS on expected gain in YLD and rank of five-trait indices calculated from ten combinations of traits

Trait[a] combination	Expected gain in YLD (q/ha)								
	0/5[b]	0.5/5	1/5	0/12	0.5/12	1/12	0/25	0.5/25	1/25
1	5.63 4[c]	5.35 2	4.95 1	4.94 4	4.63 1	4.28 1	3.59 1	3.39 1	3.18 1
2	5.87 2	5.45 1	4.91 2	4.99 2	4.55 2	4.12 2	3.53 3	3.26 3	3.01 3
3	5.87 3	5.24 3	4.51 4	5.03 1	4.52 3	3.95 3	3.56 2	3.35 2	3.07 2
4	5.88 1	5.24 4	4.45 6	4.95 3	4.33 4	3.71 7	3.52 5	3.12 6	2.76 7
5	5.48 5	5.12 5	4.67 3	4.66 6	4.32 5	3.95 4	3.29 7	3.08 7	2.87 6
6	5.45 6	5.00 6	4.48 5	4.70 5	4.27 6	3.84 5	3.52 4	3.23 4	2.96 4
7	5.30 7	4.88 7	4.41 7	4.60 7	4.20 7	3.80 6	3.47 6	3.20 5	2.94 5
8	5.03 8	4.57 8	4.10 8	4.27 8	3.87 8	3.49 8	3.17 8	2.91 8	2.68 8
9	4.66 10	4.13 9	3.65 9	3.83 10	3.42 9	3.06 9	2.68 10	2.50 10	2.31 9
10	4.73 9	4.04 10	3.44 10	3.94 9	3.39 10	2.94 10	2.87 9	2.55 9	2.28 10

[a]Combinations: 1=YLD-KWT-ER-LP-OPAC; 2=YLD-MOIST-KWT-ER-LP; 3=YLD-MOIST-KWT-ER-LYS; 4=YLD-MOIST-KWT-ER-KH; 5=YLD-ER-LP-OPAC-KWT; 6=YLD-KWT-LYS-HIST-OPAC; 7=YLD-KWT-PROT-LYS-OPAC; 8=YLD-PROT-LYS-OPAC-KQUAL; 9=YLD-KH-LYS-HIST-KQUAL; 10=YLD-MOIST-KWT-LYS-OPAC.

[b]Restrictions on gain in LP/KH, expressed as a percentage of gain in YLD; the restrictions 0.5/12 were used throughout the remainder of this study.

[c]Rank within columns.

within the range of selection goals for LP and KH considered here, the specific values used in the restrictions played a relatively small part in determining the characters to be used in an index.

The use of data from the S_0 plant (or S_1 seed) to substitute for data collected in the replicated S_1 progeny test was investigated using the most effective five- and six-trait indices of each type as a basis. The traits KH, PROT, LYS, LP, HIST, and OPAC were considered for evaluation in the S_0 generation.

The protein traits PROT, LYS, LP, and HIST were shown to have higher heritabilities on a single plant basis than KH and OPAC; in addition, they are relatively expensive to determine. Therefore, there would be particular advantages to measuring these characters in unreplicated experiments with seed from S_0 plants. Accordingly, for the S_1 recurrent selection scheme requiring three years to complete a cycle (Table 5, p. 63), KH and OPAC were considered for possible measurement on either a sample of S_1 seed or seed harvested from the replicated trials, while PROT, LYS, LP, and HIST were considered only for measurement on a single plant basis. Thus, based on the index incorporating YLD, MOIST, KWT, LYS, and OPAC (index 17-89, Tables 17-19), two indices were considered, one in which YLD, MOIST, KWT, and OPAC were measured in the replicated progeny trials and LYS was measured

on S_1 seed, and one in which YLD, MOIST, and KWT were measured in replicated trials and LYS and OPAC were determined on S_1 seed.

In the S_1 recurrent selection scheme in which a winter nursery would be employed to reduce the time needed for one cycle to two years (Table 5, p. 63), there would be insufficient time between harvest of S_1 seed in the winter nursery and planting of replicated trials to collect data, except possibly OPAC, for use in a selection index. Accordingly, only OPAC was considered for measurement in the S_0 generation.

The results of calculating indices incorporating S_1 and S_0 data are given, along with comparisons to the corresponding index utilizing replicated S_1 progeny data only, in Table 25. Transferring the determination of protein traits from the S_1 to the S_0 generation resulted in little reduction in gain in YLD with type I indices; in fact, a slight increase was achieved in one instance (25-3).[1] With type II and III indices, however, reductions in effectiveness for YLD ranged from 20 to 29%.

Measuring OPAC in the S_0 rather than the S_1 generation

[1] In this instance the lower heritability of LP when measured on an S_0 plant basis is evidently compensated for by the elimination (since S_0 and S_1 environmental effects are uncorrelated) of the environmental portions of the covariances of LP with the other traits. These covariances contribute to the phenotypic variance of the index and consequently appear in the denominator of the expression for expected gain.

Table 25. Comparison of expected gains per cycle from restricted[a] selection indices in S_1 recurrent selection that utilize data from the S_0 and S_1 generations and indices[1] that utilize S_1 data[b] only

Index no.	Restrictions[a]	Type	Traits Measured in S_1	Traits Measured in S_0	Corresponding pure S_1 index[c]	Expected gain in YLD(q/ha) S_1-S_0 index	Expected gain in YLD(q/ha) Pure S_1 index
3 years/cycle - only protein traits in S_0							
25-1	MP	I	YLD-KWT-ER-OPAC	LP	17-24	4.61	4.64
25-2		I	YLD-MOIST-KWT-ER	LYS	17-3	4.37	4.52
25-3		I	YLD-MOIST-KWT-ER-OPAC	LP	20-9	4.93	4.90
25-4	MP	I	YLD-KWT-ER-OPAC	LP-HIST	20-12	4.61	4.68
25-5		II	YLD-KWT-OPAC	LYS-HIST	17-62	3.20	4.27
25-6	P	II	YLD-KWT-OPAC	PROT-LYS	17-59	3.32	4.20
25-7	P	II	YLD-KWT-OPAC	LYS-LP	17-61	3.25	4.07
25-8	M	II	YLD-KWT-OPAC	PROT-LYS-HIST	20-26	3.22	4.41
25-9	M	III	YLD-MOIST-KWT-OPAC	LYS	17-89	2.42	3.39
25-10	M	III	YLD-MOIST-KWT-KQUAL	LYS	17-90	2.37	3.18
25-11	M	III	YLD-MOIST-KWT-KH	LYS	17-87	2.38	3.11
25-12	M	III	YLD-MOIST-KWT-OPAC-KQUAL	LYS	20-43	2.42	3.41
25-13	M	III	YLD-MOIST-KWT-KH-KQUAL	LYS	20-41	2.39	3.22

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

[b]S_1 data from two locations with two replications per location; selection intensity 20%.

[c]See Tables 17, 18 and 19 for indices with 17- prefix and Tables 20, 21 and 22 for indices with 20- prefix.

Table 25 (Continued)

Index no.	Restrictions[a]	Type	Traits Measured in S_1	Traits Measured in S_0	Corresponding pure S_1 index[c]	Expected gain in YLD (q/ha) S_1-S_0 index	Expected gain in YLD (q/ha) Pure S_1 index
3 years/cycle - protein traits, KH, and OPAC in S_0							
25-14	M	I	YLD-KWT-ER	LP-OPAC	17-24	2.65	4.64
25-15	M	I	YLD-MOIST-KWT-ER	LP-OPAC	20-9	4.65	4.90
25-16	MP	I	YLD-KWT-ER	LP-HIST-OPAC	20-12	3.04	4.68
25-17	MP	II	YLD-KWT	LYS-HIST-OPAC	17-62	2.72	4.27
25-18	M	II	YLD-KWT	PROT-LYS-OPAC	17-59	2.24	4.20
25-19	M	II	YLD-KWT	LYS-LP-OPAC	17-61	1.99	4.07
25-20	M	II	YLD-KWT	PROT-LYS-HIST-OPAC	20-26	2.75	4.41
25-21	M	III	YLD-MOIST-KWT	LYS-OPAC	17-89	2.39	3.39
25-22	M	III	YLD-MOIST-KWT-KQUAL	LYS-OPAC	20-43	2.41	3.41
25-23	M	III	YLD-MOIST-KWT-KQUAL	KH-LYS	20-41	2.38	3.22
2 years/cycle - only OPAC in S_0							
25-24	M	I	YLD-KWT-ER-LP	OPAC	17-24	2.62	4.64
25-25	M	I	YLD-MOIST-KWT-ER-LP	OPAC	20-9	4.58	4.90
25-26	MP	I	YLD-KWT-ER-LP-HIST	OPAC	20-12	3.17	4.68
25-27	M	II	YLD-KWT-LYS-HIST	OPAC	17-62	2.83	4.27
25-28	M	II	YLD-KWT-PROT-LYS	OPAC	17-59	2.42	4.20
25-29	M	II	YLD-KWT-LYS-LP	OPAC	17-61	2.27	4.07
25-30	M	II	YLD-KWT-PROT-LYS-HIST	OPAC	20-26	3.04	4.41
25-31	M	III	YLD-MOIST-KWT-LYS	OPAC	17-89	2.99	3.39
25-32	M	III	YLD-MOIST-KWT-LYS-KQUAL	OPAC	20-43	3.25	3.41

resulted in substantial reductions in effectiveness for many indices, probably because of the low heritability (0.08) for OPAC on a single plant basis. Exceptions were index 25-25 and the type III indices; in these indices the relative importance of OPAC was low (Tables 18 and 21), and contributed relatively little to effectiveness.

Indices based on S_0 determination of protein traits usually had larger weights on traits other than YLD than their pure S_1 counterparts (Table 26). Particularly striking examples were indices 25-2 (compare to 17-3) and 25-15 and 25-25 (compare to 20-9), but the trend was apparent for indices of all types. Exceptions were indices 25-1, 25-14, and 25-24, all based on 17-24. Transferring LYS from the S_1 to the S_0 generation resulted in an increase in the magnitude of the weights on LYS, KWT, and MOIST in type III indices. This was probably because heritabilities for protein quality traits were decreased by using S_0 data, while selection goals (restrictions) for LP and KH remained unchanged. Hence, weights on traits correlated with LP and KH had to be increased to maintain advance.

When OPAC was determined in the S_0 generation, weights on OPAC frequently, though not invariably, decreased. Index 25-23, which included KH as a character to be measured in the S_0 generation, had a small negative weight on KH.

Expected results from culling S_0 plants based on the S_0

Table 26. Weights of indices listed in Table 25 with weights of corresponding pure S_1 indices for comparison purposes

Index no.	Restrictions[a]	Type	Weights									
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
25-1	MP	I	1		.93	-27				50[b]		-2.0[b]	
25-14	M	I	1		-.28	-30				27[b]		-1.3[b]	
25-24	M	I	1		-.29	-30				27		-1.3[b]	
17-24	MP	I	1		.93	-27				50		-2.0	
25-2		I	1	-11.1	6.27	-174			845[b]				
17-3		I	1	-2.5	2.57	-58			511				
25-3		I	1	-1.3	3.27	-62				79[b]		-2.5[b]	
25-15	M	I	1	-20.3	28.4	-663				315[b]		-2.8[b]	
25-25	M	I	1	-23.9	33.2	-777				360		-2.9[b]	
20-9	MP	I	1	-1.0	2.93	-54				76		-2.4	
25-4	MP	I	1		.92	-27				50[b]	-7.1[b]	-2.0[b]	
25-16	MP	I	1		.08	-113				60[b]	-975[b]	-2.8[b]	
25-26	MP	I	1		-1.09	-233				75	-232	-3.9[b]	
20-12	MP	I	1		-1.00	-20				49	76.2	-1.9	
25-5		II	1		2.87				1193[b]		-1144[b]	-2.1[b]	
25-17	MP	II	1		6.88				1905[b]		-1652[b]	-2.3[b]	
25-27	M	II	1		4.09				1242		-945	-1.6[b]	
17-62		II	1		2.05				1118[b]		-1189	-2.4	
25-6	P	II	1		1.78			-22[b]	753[b]			-1.9[b]	
25-18	M	II	1		2.31			-18[b]	772[b]			-1.5[b]	
25-28	M	II	1		1.26			-8.2	550			-1.0[b]	
17-59		II	1		1.43			-21	702[b]			-1.9	
25-7	P	II	1		1.72				230[b]	43[b]		-2.0[b]	
25-19	M	II	1		.98				334[b]	15[b]		-1.1[b]	
25-29	M	II	1		.37				356	.6		-.6[b]	
17-61		II	1		1.28				246	-33		-1.7	

[a] See Table 25 for description of restrictions.

[b] Trait measured in S_0 generation.

Table 26 (Continued)

Index no.	Restrictions[a]	Type	Weights									
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
25-8	M	II	1		4.01			-23[b]	1158[b]		-278[b]	-2.1[b]	
25-20	M	II	1		6.20			12[b]	1778[b]		-1808[b]	-1.8[b]	
25-30	M	II	1		3.25			24	1115		-1420	-.8[b]	
20-26		II	1		1.86			-13	991		-679	-2.5	
25-9	M	III	1	-.6	2.05				580[b]			-.5[b]	
25-21	M	III	1	-1.0	2.91				691[b]			-.4[b]	
25-31	M	III	1	-.7	2.23				603			-.5[b]	
17-89	M	III	1	-.2	.98				439[b]			-.6	-21
25-10	M	III	1	-1.5	2.93				840[b]				-26
17-90	M	III	1	-1.0	1.25				661[b]				
25-11	M	III	1	-.9	1.95		1.20		535[b]				
17-87	M	III	1	-.6	1.05		1.30		414[b]				
25-12	M	III	1	-.7	2.05				584[b]			-.5[b]	-.7
25-22	M	III	1	-1.0	2.34				681[b]			-.3[b]	-.9
25-32	M	III	1	-.7	1.09				578			-.2[b]	-18
20-43	M	III	1	-.3	.89				458[b]			-.5	-4.4
25-13	M	III	1	-1.0	2.01		.90[b]		592[b]				-5.8
25-23	M	III	1	-1.7	3.34		-.43[b]		956[b]				-28
20-41	M	III	1	-.7	.95		.65		519				-14

portion of an index, followed by testing S_1 progenies and selecting families using the total index (incorporating both S_0 and S_1 data) are given in Table 27. The protection level markedly influenced the amount of culling permitted, with expected gains for a few type I indices exceeding gains from direct selection for YLD (6.00 q/ha) at the 25% protection level. These expected gains were probably overestimates, however, because of deviations from true truncation selection at this protection level. In two instances (indices 25-15 and 25-32) the degree of culling permitted at the 25% protection level was such that the number of S_0 plants that could be self-pollinated and evaluated, rather than the number of S_1 lines that could be tested, would probably be the limiting factor in selection effectiveness.

Several indices having low expected gains when no culling was considered (Table 25; e.g., 25-14, 25-16, 25-19, and 25-24) permitted rather high culling percentages at the 5% and 10% protection levels, while no culling could be performed at these protection levels with some of the indices having high expected gains (e.g., 25-15 and 25-25). The higher culling percentages of the former, however, did not allow them to overtake the latter in gain when culling was practiced. In fact, the ranks of the indices in expected gain were similar whether the indices were compared

Table 27. Expected gains per cycle in YLD for restricted[a] selection indices incorporating S_0 plant and S_1 progeny data[b] when culling of S_0 plants is practiced

Index no.	Type	r[d]	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
3 years/cycle - only protein traits in S_0											
25-1	I	-.42	0	100	4.61	5.7	106	4.71	77.6	446	6.95
25-2	I	-.03	.8	101	4.40	9.9	111	4.56	74.6	394	6.43
25-3	I	-.34	0	100	4.93	2.0	102	4.97	81.5	500	7.57
25-4	I	-.42	.1	100	4.61	4.8	105	4.71	77.9	452	6.98
25-5	II	-.36	26.6	136	3.57	42.0	173	3.84	69.4	327	4.53
25-6	II	-.43	20.2	125	3.60	36.9	159	3.89	69.3	326	4.70
25-7	II	-.46	15.8	119	3.46	33.1	150	3.76	69.4	327	4.60
25-8	II	-.35	12.6	114	3.38	30.0	143	3.66	69.7	330	4.55

[a] See Table 25 for restrictions.

[b] S_1 progeny data from two locations with two replications per location.

[c] Protection level (probability that an S_0 plant for which the value of the S_0 portion of the index falls at the point separating selections from discards would produce an S_1 progeny for which the value of the S_1 portion of the index was so high that the family fell into the selected class, based on the total index.

[d] Phenotypic correlation between S_0 and S_1 portions of index.

[e] Percentage of S_0 plants that could be culled based on the given protection level and a 20% selection intensity in the S_1 progeny testing stage.

[f] Number of S_0 plants to be measured if it is desired to test 100 S_1 lines; maximum of 500 S_0 plants permitted.

[g] Based on selection of 20 families using the total index.

Table 27 (Continued)

Index no.	Type	r^d	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
3 years/cycle - only protein traits in S_0 (continued)											
25-9	III	-.23	34.2	152	2.80	47.6	191	2.99	69.9	332	3.44
25-10	III	-.20	30.8	145	2.71	45.1	182	2.89	69.6	329	3.35
25-11	III	-.19	31.4	146	2.72	45.6	184	2.91	69.7	330	3.37
25-12	III	-.23	34.3	152	2.80	47.7	191	2.99	69.9	322	3.44
25-13	III	-.19	32.6	148	2.75	46.4	187	2.94	69.8	331	3.40
3 years per cycle - protein traits KH, and OPAC in S_0											
25-14	I	.01	37.5	160	3.12	49.9	200	3.33	70.2	336	3.77
25-15	I	-.15	0	100	4.65	0	100	4.65	96.7	500	7.14
25-16	I	.01	29.0	141	3.43	43.9	178	3.69	69.5	328	4.30
25-17	II	-.26	20.0	125	2.95	36.8	158	3.19	69.3	326	3.85
25-18	II	-.21	41.5	171	2.69	52.7	211	2.85	70.6	340	3.18
25-19	II	-.20	49.5	198	2.49	58.2	239	2.62	71.8	355	2.87
25-20	II	-.27	20.7	126	2.99	37.4	160	3.24	69.3	326	3.89
25-21	III	-.22	27.9	139	2.70	43.0	175	2.89	69.5	328	3.38
25-22	III	-.22	34.8	153	2.79	48.1	193	3.00	69.9	332	3.43
25-23	III	-.20	29.6	142	2.70	44.3	179	2.89	69.6	329	3.37
2 years/cycle - only OPAC in S_0											
25-24	I	-.02	35.7	156	3.07	48.6	195	3.26	70.0	333	3.72
25-25	I	-.05	0	100	4.58	0	100	4.58	99.5	500	7.03
25-26	I	.03	12.9	115	3.35	30.3	143	3.60	69.7	330	4.48

Table 27 (Continued)

Index no.	Type	r[d]	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
25-27	II	-.17	13.6	116	2.99	31.0	145	3.23	69.6	329	4.00
25-28	II	-.18	32.7	149	2.78	46.5	187	2.97	69.8	331	3.44
25-29	II	-.13	27.3	138	2.55	42.6	174	2.74	69.4	327	3.23
25-30	II	-.13	.4	100	3.04	8.1	109	3.15	75.8	413	4.52
25-31	III	-.15	0	100	2.99	3.0	103	3.03	80.1	500	4.59
25-32	III	-.15	0	100	3.25	0	100	3.25	99.9+	500	4.99

under protection levels of 5% or 10% or under conditions of no culling (as in Table 25).

Correlations between the S_0 and S_1 portions of the index were generally negative and greater in magnitude when the S_0 portion included only protein traits. In this case, portions of the index were less strongly correlated for type III indices than for types I and II. This suggested that gains associated with type III indices were less subject to overestimation caused by losses in genetic variance of the S_1 portion that might result from selection on the S_0 portion. Correlations became fairly low when OPAC was incorporated into the S_0 portion.

Indices for Full-Sib Testing

Procedures for investigating selection indices for full-sib testing were similar to those for S_1 testing. Fifty-one combinations of five traits were selected from those that had been investigated with S_1 testing (Table 17). Expected gains for the 51 combinations are shown in Table 28.

The expected gains in YLD from the most effective full-sib indices were compared with the gains from the S_1 index incorporating the same traits, in order to determine whether a combination of traits producing an effective index for S_1 testing would also be effective in full-sib testing (Table 29). Gains in YLD for the full-sib indices were approximately

Table 28. Expected gain per cycle in YLD for 51 five-trait restricted[a] selection indices in full-sib recurrent selecting with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
28-1	I		X	X	X	X	X							2.70
28-2	I	P	X	X	X	X		X						2.62
28-3	I		X	X	X	X			X					2.91
28-4	I	M	X	X	X	X				X				2.90
28-5	I		X	X	X	X						X		2.68
28-6	I		X	X	X	X							X	2.60
28-7	I	M	X	X		X	X			X				2.53
28-8	I		X	X		X			X				X	2.62
28-9	I	M	X	X		X				X		X		2.51
28-10	I	M	X	X		X				X			X	2.69
28-11	I	MP	X		X	X				X		X		2.83
28-12	I	M	X			X		X	X			X		2.58
28-13	I	M	X			X			X	X		X		2.50
28-14	I	M	X			X			X		X	X		2.55
28-15	I	MP	X			X				X		X	X	2.65
28-16	II	M	X	X			X	X	X					1.74
28-17	II	M	X	X			X		X		X			1.87
28-18	II	M	X	X				X	X			X		1.82
28-19	II	M	X	X				X	X				X	1.77
28-20	II	M	X	X					X	X		X		1.75
28-21	II	M	X	X					X		X	X		1.91
28-22	II	M	X	X					X		X		X	1.81
28-23	II	M	X		X		X		X		X			2.27
28-24	II		X		X			X	X			X		2.44
28-25	II	M	X		X			X		X		X		2.32
28-26	II		X		X				X	X		X		2.38
28-27	II		X		X				X		X	X		2.62
28-28	II		X				X	X	X		X			1.86
28-29	II		X				X	X	X			X		1.87
28-30	II		X				X	X		X		X		1.74
28-31	II		X				X		X	X	X			1.84
28-32	II		X				X		X	X		X		1.79
28-33	II		X				X		X		X	X		1.93
28-34	II		X				X		X		X		X	2.10

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices, restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

Table 28 (Continued)

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
28-35	II		X					X	X		X	X		1.78
28-36	II		X					X	X			X	X	2.19
28-37	II		X					X		X		X	X	2.04
28-38	II		X						X	X	X		X	1.86
28-39	II		X						X	X		X	X	2.10
28-40	II		X						X		X	X	X	2.20
28-41	III	M	X	X	X		X		X					1.94
28-42	III	MP	X	X	X		X			X				1.63
28-43	III	M	X	X	X				X			X		2.08
28-44	III	M	X	X	X				X				X	1.97
28-45	III	MP	X	X	X					X		X		.46
28-46	III	MP	X	X	X					X			X	.13
28-47	III	M	X	X					X			X	X	1.82
28-48	III	M	X		X		X		X				X	.92
28-49	III	MP	X		X		X			X		X		1.52
28-50	III	M	X		X		X			X			X	.83
28-51	III	P	X		X					X		X	X	.15

40% lower than those of their S_1 counterparts, reflecting the lower genetic variance among full-sib families. Ranks of combinations within an index type were very similar for the two breeding schemes; the schemes agreed in the choice of the best four indices within each type. There was also good agreement with respect to the restrictions required in each index.

Weights for the most effective five-trait indices for full-sib testing are given in Table 30. Weights were similar to those of the corresponding S_1 indices (Table 18), except that weights and importance relative to YLD for

Table 29. Comparison of expected gain per cycle in YLD of the most effective five-trait indices of each type for full-sib selection with the gain for the S_1 index incorporating the same traits

Full-sib Index					S_1 Index			
Index no.	Type	Restrictions[a]	Gain in YLD (q/ha)	Rank[b]	Index no.	Restrictions[a]	Gain in YLD (q/ha)	Rank[c]
28-3	I		2.91	1	17-3		4.52	3
28-4	I	M	2.90	2	17-4	M	4.55	2
28-11	I	MP	2.83	3	17-24	MP	4.64	1
28-1	I		2.70	4	17-1	M	4.33	4
28-10	I	M	2.69	5	17-22	M	4.27	6
28-27	II		2.62	1	17-62		4.27	1
28-24	II		2.44	2	17-59		4.20	2
28-26	II		2.38	3	17-61		4.07	3
28-25	II	M	2.32	4	17-60		3.97	4
28-23	II	M	2.27	5	17-57	M	3.55	9
28-43	III	M	2.08	1	17-89	M	3.39	1
28-44	III	M	1.97	2	17-90	M	3.18	2
28-41	III	M	1.94	3	17-87	M	3.11	3
28-47	III	M	1.82	4	17-97	M	3.08	4

[a]See Table 28 for description of restrictions.

[b]Rank in gain in YLD among indices of the same type in Table 28.

[c]Rank in gain in YLD among indices of the same type (excluding those calculated from nonpositive-definite matrices) in Table 17.

Table 30. Weights of five-trait indices from Table 28 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD (q/ha)	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
28-3	I		2.91	1	-2.7	2.83	-58			547				
28-4	I	M	2.90	-1	-31.7	43.2	-965				387			
28-11	I	MP	2.83	1		.93	-27				49.7		-2.0	
28-1	I		2.70	-1	-2.9	3.41	-99	-4.3						
28-27	II		2.62	1		2.56				1252		-1346	-2.5	
28-24	II		2.44	1		1.63			-18	700			-1.7	
28-26	II		2.38	1		1.54				285	31.3		-1.6	
28-25	II	M	2.32	1		1.56			11		56.5		-1.8	
28-43	III	M	2.08	1	-.3	1.24				474			-.5	
28-44	III	M	1.97	1	-1.2	1.83				723				-25
28-41	III	M	1.94	1	-.7	1.42		1.3		464				
28-47	III	M	1.82	1	-.2					410			-.3	-14
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				7.0	2.3	6.3	.46	2.0	.49	.023	.21	.014	5.3	.32

[a] See Table 28 for description of restrictions.

[b] Phenotypic standard deviation (full-sib family basis).

MOIST, KWT, and LYS were often slightly higher, especially in type III indices. For example, the index 28-43 (YLD - 0.3 MOIST + 1.24 KWT + 474 LYS - 0.5 OPAC) corresponded to the S_1 index 17-89 (YLD - 0.2 MOIST + 0.98 KWT + 439 LYS - 0.6 OPAC). Importance of MOIST, KWT, LYS, and OPAC relative to YLD was 0.10, 1.1, 1.6, and 0.4, respectively, for index 28-43, and 0.07, 1.0, 1.5, and 0.5, respectively, for index 17-89.

Expected gains in all traits for the most effective full-sib indices are shown in Table 31. Gains were generally in the proportions observed previously with the corresponding S_1 indices, i.e., gain in each character was 30 to 50% lower than that obtained from the S_1 counterpart.

The results of calculating six-trait indices are shown in Tables 32, 33, and 34. The incorporation of a sixth trait was of little value in increasing the genetic gain of a type III index and of only slightly greater value to a type I or II index. As with five-trait indices, the most effective six-trait combinations for full-sib testing were generally the most effective for S_1 testing as well. Weights given to MOIST, KWT, KH, and LYS by six-trait, full-sib indices were generally slightly higher than those of the corresponding S_1 indices.

The most effective five- and six-trait indices formed

Table 31. Expected gains per cycle from five-trait indices listed in Table 30

Index no.	Type	Restrictions[a]	Expected Gain										
			YLD g/ha	MOIST %	KWT %	ER	KH	PROT %	LYS %	LP g/100 g	HIST %	OPAC %	KQUAL
28-3	I		2.91	-.1	2.9	-.30	.35	.12	.007	.01	.002	1.1	-.09
28-4	I	M	2.90	.0	3.2	-.28	.35	.04	.003	.01	-.001	1.0	-.10
28-11	I	MP	2.83	.0	.8	-.29	.34	.00	.002	.01	-.001	-.7	-.05
28-1	I		2.70	.0	2.3	-.29	.32	.05	.003	.01	-.001	.9	-.08
28-27	II		2.62	-.3	3.5	-.16	.31	.04	.003	.01	-.001	.5	-.10
28-24	II		2.44	-.1	3.6	-.11	.29	.02	.002	.01	.001	.4	-.07
28-26	II		2.38	.0	3.6	-.12	.29	.04	.003	.01	.001	.5	-.07
28-25	II		2.32	.0	3.6	-.11	.28	.03	.003	.01	.001	.4	-.07
28-43	III	M	2.08	.0	3.6	-.13	.25	.17	.008	.01	.004	1.2	-.07
28-44	III	M	1.97	.0	4.3	-.11	.24	.14	.007	.01	.003	1.9	-.11
28-41	III	M	1.94	.0	4.3	-.12	.23	.15	.007	.01	.004	1.6	-.09
28-47	III	M	1.82	.0	.8	-.19	.22	.19	.009	.01	.004	.5	-.05

[a]See Table 28 for description of restrictions.

Table 32. Expected gain per cycle in YLD for 22 six-trait restricted[a] selection indices in full-sib recurrent selection with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
32-1	I	M	X	X	X	X	X		X					2.94
32-2	I	M	X	X	X	X			X	X				2.96
32-3	I	M	X	X	X	X			X		X			3.00
32-4	I		X	X	X	X			X			X		2.91
32-5	I		X	X	X	X			X				X	2.92
32-6	I	M	X	X	X	X				X		X		3.06
32-7	I	M	X	X	X	X				X			X	2.96
32-8	I	MP	X		X	X				X	X	X		2.84
32-9	I	MP	X		X	X				X		X	X	2.84
32-10	II	M	X	X	X			X	X			X		2.46
32-11	II	M	X	X	X				X		X	X		2.69
32-12	II		X		X			X	X		X	X		2.66
32-13	II		X		X			X	X			X	X	2.52
32-14	II		X		X			X		X	X	X		2.50
32-15	II		X		X				X	X	X	X		2.64
32-16	II	M	X		X				X	X		X	X	2.45
32-17	II		X		X				X		X	X	X	2.68
32-18	III	MP	X	X	X		X			X		X		1.63
32-19	III	M	X	X	X		X		X				X	1.99
32-20	III	MP	X	X	X		X			X			X	1.63
32-21	III	M	X	X	X				X			X	X	2.08
32-22	III	MP	X	X	X					X		X	X	.47

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

Table 33. Weights of six-trait indices from Table 32 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD (q/ha)	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
32-6	I	M	3.06	1	-1.5	4.01	-69				89.6		-2.7	
32-3	I	M	3.00	1	-5.7	10.2	-189			1788		-1516		
32-2	I	M	2.96	1	-4.1	5.6	-111			571	25.2			
32-7	I	M	2.96	-1	-2.5	26	-688				419			-244
32-11	II	M	2.69	1	1.3	2.20				1174		-1367	-2.2	
32-17	II		2.68	1		2.45				1454		-1602	-2.6	-15
32-12	II		2.66	1		2.45			-9.6	1179		-1010	-2.7	
32-15	II		2.64	1		2.44				1028	13.1	-1089	-2.6	
32-21	III	M	2.08	1	-.4	1.17				491			-.5	-4
32-19	III	M	1.99	1	-.8	1.35		.70		554				-12
32-18	III	MP	1.63	1	-.4	.17		4.13			30.7		.04	
32-20	III	MP	1.63	1	-.3	.14		4.02			30.5			.04
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				7.0	2.3	6.3	.46	2.0	.49	.023	.21	.014	5.3	.32

[a] See Table 32 for description of restrictions.

[b] Phenotypic standard deviation (full-sib family basis).

Table 34. Expected gains per cycle from six-trait indices listed in Table 32

Index no.	Type	Restrictions[a]	Expected Gain										
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
			g/ha	%	g			%	%	g 100/g	%	%	
32-6	I	M	3.06	.0	3.0	-.27	.37	.00	.002	.02	-.001	.4	-.09
32-3	I	M	3.00	.0	3.4	-.29	.36	.08	.005	.01	.000	1.2	-.11
32-2	I	M	2.96	.0	3.3	-.29	.36	.09	.005	.01	.001	1.2	-.10
32-7	I	M	2.96	.0	3.1	-.29	.36	.02	.003	.01	-.001	1.1	-.12
32-11	II	M	2.69	.0	3.5	-.18	.32	.04	.002	.01	-.001	.5	-.11
32-17	II		2.68	-.3	3.4	-.17	.32	.04	.002	.01	-.001	.6	-.12
32-12	II		2.66	-.3	3.5	-.14	.32	.01	.001	.01	-.001	.3	-.10
32-15	II		2.64	-.3	3.5	-.15	.32	.02	.002	.01	-.001	.4	-.10
32-21	III	M	2.08	.0	3.5	-.14	.25	.17	.008	.01	.004	1.3	-.07
32-19	III	M	1.99	.0	4.1	-.12	.24	.15	.007	.01	.003	1.7	-.10
32-18	III	MP	1.63	.0	2.2	-.16	.20	.00	.002	.01	.000	-.1	-.08
32-20	III	MP	1.63	.0	2.0	-.16	.20	.00	.002	.01	.000	-.2	-.08

[a]See Table 32 for description of restrictions.

the basis for the study of the effect of measuring some characters on the single plant parent (or the crossed seed produced on the parent) rather than in the replicated progeny tests (Table 35). Gains in YLD for type II and III indices when single-plant data were incorporated were 58 to 65% of the gains from the corresponding pure full-sib progeny indices. When the determination of OPAC or KH in addition to the protein traits was shifted from the progeny tests to single plants, gains were little affected.

Compared to their pure full-sib counterparts, most full-sib single plant indices had weights that shifted a greater portion of the selection pressure away from YLD (Table 36). Some type I indices (35-1, 35-3, and 35-14) displayed severe shifts in the weights. The full-sib single plant counterparts of type I index 28-11 were unusual in that one (35-2) had smaller weights for characters other than YLD than did 28-11, while the other (35-13) had a negative weight for KWT. Type III indices showed substantial shifts of weight to MOIST, KWT, and LYS on conversion to full-sib single plant indices.

Expected results of culling individual plants before progeny testing are given in Table 37; indices 35-1, 35-3, 35-13, and 35-14 were excluded from this table because of their undesirable weights. In comparison to S_1-S_0 indices (Table 27), full-sib single plant indices showed lower

Table 35. Comparison of expected gains per cycle from restricted[a] selection indices in full-sib recurrent selection that utilize data from single plants and full-sib progenies and indices that utilize full-sib progeny data[b] only

Index no.	Restrictions[a]	Type	Traits: Measured on progeny	Traits: Measured on single plants	Corresponding pure full-sib progeny index[c]	Expected Gain in YLD (g/ha): Full-sib progeny single plant index	Expected Gain in YLD (g/ha): Pure full-sib progeny index
Only protein traits on single plants							
35-1		I	YLD-MOIST-KWT-ER	LYS	28-3	2.67	2.91
35-2	M	I	YLD-KWT-ER-OPAC	LP	28-11	2.22	2.83
35-3	M	I	YLD-MOIST-KWT-ER-OPAC	LP	32-6	2.83	3.06
35-4		II	YLD-KWT-OPAC	LYS-HIST	28-27	1.56	2.62
35-5	M	II	YLD-MOIST-KWT-OPAC	LYS-HIST	32-11	1.57	2.69
35-6	M	II	YLD-KWT-OPAC-KQUAL	LYS-HIST	32-17	1.58	2.68
35-7	P	II	YLD-KWT-OPAC	PROT-LYS-HIST	32-12	1.64	2.66
35-8	M	III	YLD-MOIST-KWT-OPAC	LYS	28-43	1.26	2.08
35-9	M	III	YLD-MOIST-KWT-KQUAL	LYS	28-44	1.26	1.97
35-10	M	III	YLD-MOIST-KWT-KH	LYS	28-41	1.26	1.94
35-11	M	III	YLD-MOIST-KWT-OPAC-KQUAL	LYS	32-21	1.26	2.08
35-12	M	III	YLD-MOIST-KWT-KH-KQUAL	LYS	32-19	1.26	1.99

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

[b]Full-sib progeny data from two locations with two replications per location; selection intensity 20%.

[c]See Tables 28, 30, and 31 for indices with 28- prefix and Tables 32, 33 and 34 for indices with 32- prefix.

Table 35 (Continued)

Index no.	Restrictions[a]	Type	Traits: Measured on progeny	Traits: Measured on single plants	Corresponding pure full-sib progeny index[c]	Expected Gain in YLD (q/ha): Full-sib progeny single plant index	Expected Gain in YLD (q/ha): Pure full-sib progeny index
Protein and other traits on single plants							
35-13	M	I	YLD-KWT-ER	LP-OPAC	28-11	1.48	2.83
35-14	M	I	YLD-MOIST-KWT-ER	LP-OPAC	32-6	2.83	3.06
35-15	M	II	YLD-KWT	LYS-HIST-OPAC	28-27	1.45	2.62
35-16	M	II	YLD-MOIST-KWT	LYS-HIST-OPAC	32-11	1.50	2.69
35-17	M	II	YLD-KWT-KQUAL	LYS-HIST-OPAC	32-17	1.55	2.68
35-18	M	II	YLD-KWT	PROT-LYS-HIST-OPAC	32-12	1.46	2.66
35-19	M	III	YLD-MOIST-KWT	LYS-OPAC	28-43	1.27	2.08
35-20	M	III	YLD-MOIST-KWT	KH-LYS	28-41	1.26	1.94
35-21	M	III	YLD-MOIST-KWT-KQUAL	LYS-OPAC	32-21	1.27	2.08
35-22	M	III	YLD-MOIST-KWT-KQUAL	KH-LYS	32-19	1.27	1.99

Table 36. Weights of indices listed in Table 35, with weights of corresponding pure full-sib indices for comparison purposes

Index no.	Restrictions[a]	Type	Weights										
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
35-1		I	1	-8282	3666	-112416			334170[b]				
28-3		I	1	-2.7	2.83	-58			547				
35-2	M	I	1		.64	-28				44.3[b]		-1.8	
35-13	M	I	1		-.85	-32				16.1[b]		-.9[b]	
28-11	MP	I	1		.93	-27				49.7		-2.0	
35-3	M	I	1	-26.5	35.9	-859				380[b]		-2.5	
35-14	M	I	1	-40.9	55.2	-1314				563[b]		-2.9[b]	
32-6	M	I	1	-1.5	4.01	-69				89.6		-2.7	
35-4		II	1		6.61				1922[b]		-1756[b]	-2.5	
35-15	M	II	1		23.0				4877[b]		-3921[b]	-3.2[b]	
28-27		II	1		2.56				1252		-1346	-2.5	
35-5	M	II	1	.5	5.32				1671[b]		-1580[b]	-2.3	
35-16	M	II	1	-5.3	46.5				9787[b]		-8105[b]	-7.9[b]	
32-11		II	1	1.3	2.20				1174		-1367	-2.2	
35-6	M	II	1		6.66				2266[b]		-2086[b]	-2.2	-30
35-17	M	II	1		8.64				3787[b]		-3834[b]	-2.8[b]	-105
32-17		II	1		2.45				1454		-1602	-2.6	-15
35-7	P	II	1		5.36			-23.2[b]	1590[b]		-858[b]	-2.9	
35-18	M	II	1		15.57			15.3[b]	4007[b]		-4278[b]	-4.1[b]	
32-12		II	1		2.45			-9.6	1179		-1010	-2.7	
35-8	M	III	1	-2.0	5.67				1051[b]			-.2	
35-19	M	III	1	-1.7	4.94				957[b]			-.3[b]	
28-43	M	III	1	-.3	1.24				474			-.5	
35-9	M	III	1	-2.2	5.51				1116[b]				-12
28-44	M	III	1	-1.2	1.83				723				-25

[a]See Table 35 for description of restrictions.

[b]Trait measured on single plant basis.

Table 36 (Continued)

Index no.	Restrictions[a]	Type	Weights									
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
35-10	M	III	1	-1.7	4.30		.8[b]		851[b]				
35-20	M	III	1	-3.7	10.29		-.2[b]		1659[b]				
28-41	M	III	1	-.7	1.42		1.3		464[b]				
35-11	M	III	1	-2.5	5.96				1205[b]			.1[b]	-16
35-21	M	III	1	-1.7	4.53				932[b]			-.2[b]	-4
32-21	M	III	1	-.4	1.17				491[b]			-.5	-4
35-12	M	III	1	-1.8	4.49		.5[b]		918[b]				-5
35-22	M	III	1	-3.9	9.27		-2.1[b]		1879[b]				-43
32-19	M	III	1	-.8	1.35		.7		554				-12

Table 37. Expected gains per cycle in YLD for restricted[a] selection indices incorporating single plant and full-sib progeny data[b] when culling of single plants is practiced

Index no.	Type	r[d]	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
Only protein traits on single plants											
35-2	I	-.10	15.7	119	2.36	33.0	149	2.55	69.5	327	3.14
35-4	II	-.14	35.7	156	1.83	48.7	195	1.94	70.0	333	2.22
35-5	II	-.14	37.6	160	1.85	50.0	200	1.97	70.2	335	2.23
35-6	II	-.13	37.9	161	1.86	50.2	201	1.99	70.2	336	2.25
35-7	II	-.15	32.8	149	1.89	46.6	187	2.01	69.8	331	2.33
35-8	III	-.10	37.7	161	1.48	50.1	200	1.58	70.2	335	1.79
35-9	III	-.10	38.0	161	1.49	50.9	204	1.59	70.3	337	1.79
35-10	III	-.09	38.9	164	1.49	50.9	204	1.59	70.3	337	1.79
35-11	III	-.10	37.6	160	1.49	50.6	202	1.58	70.3	336	1.79
35-12	III	-.10	39.5	165	1.49	51.3	205	1.59	70.4	338	1.79

[a] See Table 35 for restrictions.

[b] Full-sib progeny data from two locations with two replications per location.

[c] Protection level (probability that a single plant for which the value of the single plant portion of the index falls at the point separating selections from discards would produce a full-sib progeny for which the value of the full-sib progeny portion of the index was so high that the family fell into the selected class, based on the total index).

[d] Phenotypic correlation between single plant and full-sib progeny portions of the index.

[e] Percentage of single plants that could be culled based on the given protection level and a 20% selection intensity in the full-sib progeny testing stage.

[f] Number of single plants to be measured if it is desired to test 100 full-sib progenies; maximum of 500 single plants permitted.

[g] Based on selection of 20 families using the total index.

Table 37 (Continued)

Index no.	Type	r[d]	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
Protein and other traits on single plants											
35-15	II	-.14	33.4	150	1.68	47.0	189	1.79	69.8	331	2.06
35-16	II	-.14	24.0	132	1.66	40.0	167	1.79	69.3	326	2.12
35-17	II	-.13	38.8	163	1.84	50.8	203	1.95	70.3	337	2.20
35-18	II	-.14	34.0	151	1.69	47.4	190	1.80	69.8	332	2.08
35-19	III	-.11	38.0	161	1.50	50.3	201	1.60	70.2	336	1.81
35-20	III	-.09	33.1	149	1.45	46.8	188	1.56	69.8	331	1.79
35-21	III	-.11	39.3	165	1.51	51.2	205	1.61	70.4	337	1.81
35-22	III	-.11	36.8	158	1.49	49.4	198	1.59	70.1	334	1.81

magnitudes of correlation between the single plant and progeny portions of the index, probably because the degree of genetic relationship between a single plant and its full-sib progeny is lower than that between a plant and its selfed progeny. Perhaps as a consequence of the less negative correlation between single plant and progeny scores, higher culling percentages were permitted by the full-sib single plant indices. There was a remarkable similarity among indices of all types with respect to culling percentages, especially at the 25% protection level.

Indices for S_2 Testing

The value of a combination of traits in S_1 testing was used as a guide in selecting combinations for S_2 testing. Thus, indices for 26 five-trait combinations were considered for S_2 testing (Table 38).

The most effective combinations of each type were those that had also been effective in S_1 testing (Table 39). Gains in YLD were approximately 30% greater than gains from S_1 indices. Weights of the most effective indices (Table 40) were similar to those of their S_1 counterparts, except that the S_2 indices generally had smaller weights for MOIST, KWT, and LYS. Expected gains (Table 41) were generally in proportion to those of S_1 and full-sib indices.

Results with six-trait indices are given in Tables 42,

Table 38. Expected gain per cycle in YLD for 26 five-trait restricted[a] selection indices in S_2 recurrent selection with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD (q/ha)
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
38-1	I	M	X	X	X	X	X							5.63
38-2	I	P	X	X	X	X		X						5.48
38-3	I		X	X	X	X			X					5.77
38-4	I	M	X	X	X	X				X				5.85
38-5	I		X	X	X	X						X		5.46
38-6	I		X	X	X	X							X	5.38
38-7	I	M	X	X		X	X			X				5.23
38-8	I		X	X		X			X				X	5.31
38-9	I	M	X	X		X				X			X	5.50
38-10	I	MP	X		X	X				X		X		6.05
38-11	I		X			X		X	X			X		5.38
38-12	I	MP	X			X				X		X	X	5.61
38-13	II	M	X		X		X		X		X			4.55
38-14	II		X		X			X	X			X		5.69
38-15	II		X		X			X		X		X		5.25
38-16	II		X		X				X	X		X		5.42
38-17	II		X		X				X		X	X		5.56
38-18	II		X				X		X		X		X	4.51
38-19	II		X					X	X			X	X	5.34
38-20	II		X					X		X		X	X	4.89
38-21	II		X						X	X		X	X	5.06
38-22	II		X						X		X	X	X	4.85
38-23	III	M	X	X	X		X		X					4.03
38-24	III	MP	X	X	X		X			X				3.92
38-25	III	M	X	X	X				X			X		4.45
38-26	III	M	X	X	X				X				X	4.18

[a]The restriction that gains in YLD, KH and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

Table 39. Comparison of expected gain per cycle in YLD of the most effective five-trait indices of each type for S_2 selection with the gain for the S_1 index incorporating the same traits

S_2 Index					S_1 Index			
Index no.	Type	Restrictions[a]	Gain in YLD q/ha	Rank[b]	Index no	Restrictions[a]	Gain in YLD q/ha	Rank[c]
38-10	I	MP	6.05	1	17-24	MP	4.64	1
38-4	I	M	5.85	2	17-4	M	4.55	2
38-3	I		5.77	3	17-3		4.52	3
38-1	I	M	5.63	4	17-1	M	4.33	4
38-12	I	MP	5.61	5	17-35	MP	4.32	5
38-14	II		5.69	1	17-59		4.20	2
38-17	II		5.56	2	17-62		4.27	1
38-16	II		5.42	3	17-61		4.07	3
38-19	II		5.34	4	17-79		3.87	5
38-15	II		5.25	5	17-60		3.97	4
38-25	III	M	4.45	1	17-89	M	3.39	1
38-26	III	M	4.18	2	17-90	M	3.18	2
38-23	III	M	4.03	3	17-87	M	3.11	3

[a]See Table 38 for description of restrictions.

[b]Rank in gain in YLD among indices of the same type in Table 38.

[c]Rank in gain in YLD among indices of the same type (excluding those calculated from nonpositive-definite matrices) in Table 17.

Table 40. Weights of five-trait indices from Table 38 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD q/ha	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
38-10	I	MP	6.05	1		.94	-27				49.9		-2.0	
38-4	I	M	5.85	1	-91	115	-2911				1064			
38-3	I		5.77	1	-2.5	2.44	-59			492				
38-1	I	M	5.63	-1	-2.7	3.45	-99	-4.5						
38-14	II		5.69	1		1.24			-19	664			-1.9	
38-17	II		5.56	1		1.78				1036		-1083	-2.2	
38-16	II		5.42	1		1.16				239	31.8		-1.7	
38-19	II		5.34	1					-20	675			-1.4	-25
38-25	III	M	4.45	1	-.2	.85				423			-.6	
38-26	III	M	4.18	1	-.9	.96				629				-27
38-23	III	M	4.03	1	-.5	.88		1.4		390				
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				9.7	3.6	10.3	.66	2.9	.73	.034	.29	.021	7.6	.45

[a] See Table 38 for description of restrictions.

[b] Phenotypic standard deviation (S_2 family basis).

Table 41. Expected gains per cycle from five-trait indices listed in Table 40

Index no.	Type	Restrictions[a]	Expected Gain										
			YLD g/ha	MOIST %	KWT g	ER	KH	PROT %	LYS %	LP g/100 g	HIST %	OPAC %	KQUAL
38-10	I	MP	6.05	.0	1.6	-.62	.73	.0	.004	.03	-.003	-1.5	-.10
38-4	I	M	5.85	.0	5.7	-.60	.70	.08	.007	.03	-.002	1.8	-.19
38-3	I		5.77	-.1	5.0	-.62	.69	.25	.014	.03	.003	1.8	-.16
38-1	I	M	5.63	.0	4.8	-.60	.68	.10	.007	.03	-.002	1.9	-.16
38-14	II		5.69	-.4	6.0	-.28	.68	.02	.003	.03	.000	-.4	-.11
38-17	II		5.56	-.7	5.8	-.39	.67	.12	.007	.03	-.001	.2	-.18
38-16	II		5.42	-.2	6.1	-.30	.65	.08	.006	.03	.002	-.2	-.11
38-19	II		5.34	-.3	1.2	-.40	.64	.04	.004	.03	-.002	-1.1	-.14
38-25	III	M	4.45	.0	5.8	-.34	.53	.40	.019	.02	.010	1.9	-.11
38-26	III	M	4.18	.0	7.3	-.29	.50	.33	.016	.02	.006	3.5	-.22
38-23	III	M	4.03	.0	7.2	-.31	.48	.36	.017	.02	.009	2.6	-.16

[a]See Table 38 for description of restrictions.

Table 42. Expected gain per cycle in YLD for 20 six-trait restricted[a] selection indices in S_2 recurrent selection with testing at two locations, two replications per location, and a selection intensity of 20%

Index no.	Type	Restrictions[a]	Traits Included in Index											Gain in YLD q/ha
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL	
42-1	I	M	X	X	X	X	X		X					5.84
42-2	I	M	X	X	X	X			X	X				5.89
42-3	I	M	X	X	X	X			X		X			5.89
42-4	I		X	X	X	X			X			X		5.77
42-5	I		X	X	X	X			X				X	5.77
42-6	I	MP	X	X	X	X				X		X		6.34
42-7	I	M	X	X	X	X				X			X	5.94
42-8	I	MP	X		X	X				X	X	X		6.13
42-9	I	MP	X		X	X				X		X	X	6.06
42-10	II	M	X	X	X			X	X			X		5.75
42-11	II	M	X	X	X				X		X	X		5.69
42-12	II		X		X			X	X		X	X		5.86
42-13	II	M	X		X			X	X			X	X	5.66
42-14	II		X		X				X	X	X	X		5.66
42-15	II		X		X				X	X		X	X	5.67
42-16	II		X		X				X		X	X	X	5.64
42-17	III	M	X	X	X		X		X				X	4.22
42-18	III	MP	X	X	X		X			X		X		3.93
42-19	III	MP	X	X	X		X			X			X	3.94
42-20	III		X	X	X				X			X	X	4.49

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

43, and 44. The addition of a sixth trait increased gain relatively little in type III combinations. As before, the best six-trait combinations for S_2 testing were among the most effective for S_1 testing as well (Table 21).

Substitution of data from the parental S_1 plant for S_2 progeny data was investigated as before (Tables 45, 46, and 47).

Table 43. Weights of six-trait indices from Table 42 that have high expected gains for YLD

Index no.	Type	Restrictions[a]	Gain in YLD q/ha	Weights										
				YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
42-6	I	MP	6.34	1	-.8	2.62	-50				71.8		-2.4	
42-8	I	MP	6.13	1		1.02	-19				48.9	93.2	-1.9	
42-9	I	MP	6.06	1		1.14	-27				49.7		-2.0	3.8
42-7	I	M	5.94	-1	-157	154	-4555				2607			-1574
42-12	II		5.86	1		1.57			-15	883		-479	-2.3	
42-10	II	M	5.75	1	.5	1.10			-19	630			-1.7	
42-11	II	M	5.69	1	1.2	1.51				975		-1108	-1.9	
42-15	II		5.67	1		.91				241	38.6		-1.7	-13
42-20	III		4.49	1	-.3	.74				447			-.5	-5.4
42-17	III	M	4.22	1	-.7	.75		.59		507				-16
Population mean				64.8	23.0	77.9	1.87	61.1	8.68	.376	4.35	.237	91.5	2.92
Std. dev.[b]				9.7	3.6	10.3	.66	2.9	.73	.034	.29	.021	7.6	.45

[a] See Table 42 for description of restrictions.

[b] Phenotypic standard deviation (S_2 family basis).

Table 44. Expected gains per cycle from six-trait indices listed in Table 43

Index no.	Type	Restrictions[a]	Expected Gain										
			YLD g/ha	MOIST %	KWT g	ER	KH	PROT %	LYS %	LP g/100 g	HIST %	OPAC %	KQUAL
42-6	I	MP	6.34	.0	5.0	-.58	.76	.00	.003	.03	-.003	.2	-.16
42-8	I	MP	6.13	.0	2.8	-.56	.74	.00	.004	.03	-.002	-1.3	-.10
42-9	I	MP	6.06	.0	2.1	-.61	.73	.00	.004	.03	-.003	-1.4	-.10
42-7	I	M	5.94	.0	5.7	-.60	.71	.06	.006	.03	-.003	1.9	-.22
42-12	II		5.86	-.7	5.9	-.33	.70	.01	.003	.03	-.002	-.5	-.15
42-10	II	M	5.75	.0	5.9	-.30	.69	.01	.003	.03	.000	-.4	-.12
42-11	II	M	5.69	.0	5.7	-.43	.68	.11	.006	.03	-.001	.4	-.21
42-15	II		5.67	-.1	5.9	-.33	.68	.05	.005	.03	-.001	.2	-.17
42-20	III		4.49	.0	5.7	-.35	.54	.40	.019	.02	.009	2.1	-.13
42-17	III	M	4.22	.0	6.8	-.32	.51	.36	.017	.02	.007	3.1	-.20

[a]See Table 42 for description of restrictions.

Table 45. Comparison of expected gains per cycle from restricted[a] selection indices in S_2 recurrent selection that utilize data from single S_1 plants and S_2 progenies and indices that utilize S_2 progeny data[b] only

Index no.	Restrictions[a]	Type	Traits Measured on S_2 progeny	Traits Measured on S_1 plants	Corresponding pure S_2 index[c]	Expected gain in YLD (q/ha) S_2-S_1 Index	Expected gain in YLD (q/ha) Pure S_2 Index
Only protein traits on S_1 plants							
45-1	MP	I	YLD-KWT-ER-OPAC	LP	38-10	5.91	6.05
45-2		I	YLD-MOIST-KWT-ER-OPAC	LP	42-6	6.28	6.34
45-3	MP	I	YLD-KWT-ER-OPAC	LP-HIST	42-8	5.91	6.13
45-4	M	II	YLD-KWT-OPAC	PROT-LYS	38-14	4.21	5.69
45-5	M	II	YLD-KWT-OPAC	PROT-LYS-HIST	42-12	4.22	5.86
45-6	MP	II	YLD-MOIST-KWT-OPAC	PROT-LYS	42-10	4.51	5.75
45-7	M	III	YLD-MOIST-KWT-OPAC	LYS	38-25	3.31	4.45
45-8	M	III	YLD-MOIST-KWT-KQUAL	LYS	38-26	3.25	4.18
45-9	M	III	YLD-MOIST-KWT-KH	LYS	38-23	3.23	4.03
45-10	M	III	YLD-MOIST-KWT-OPAC-KQUAL	LYS	42-20	3.31	4.49
45-11	M	III	YLD-MOIST-KWT-KH-KQUAL	LYS	42-17	3.27	4.22

[a]The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST (M) or PROT (P) remain unchanged were used when otherwise MOIST would increase or PROT decrease.

[b]S_2 progeny data from two locations with two replications per location, selection intensity 20%.

[c]Tables 38, 40, and 41 for indices with 38 prefix and Tables 42, 43 and 44 for indices with 42- prefix.

Table 45 (Continued)

Index no.	Restrictions[a]	Type	Traits: Measured on S_2 progeny	Traits: Measured on S_1 plants	Corresponding pure S_2 index[c]	Expected gain in YLD (q/ha): S_2-S_1 Index	Expected gain in YLD (q/ha): Pure S_2 Index
Protein and other traits on S_1 plants							
45-12	M	I	YLD-KWT-ER	LP-OPAC	38-10	3.71	6.05
45-13	M	I	YLD-MOIST-KWT-ER	LP-OPAC	42-6	5.95	6.34
45-14	MP	I	YLD-KWT-ER	LP-HIST-OPAC	42-8	4.17	6.13
45-15	M	II	YLD-KWT	PROT-LYS-OPAC	38-14	3.23	5.69
45-16	M	II	YLD-KWT	PROT-LYS-HIST-OPAC	42.12	3.69	5.86
45-17	M	II	YLD-MOIST-KWT	PROT-LYS-OPAC	42-10	3.45	5.75
45-18	M	III	YLD-MOIST-KWT	LYS-OPAC	38-25	3.25	4.45
45-19	M	III	YLD-MOIST-KWT	KH-LYS	38-23	3.11	4.03
45-20	M	III	YLD-MOIST-KWT-KQUAL	LYS-OPAC	42-20	3.31	4.49
45-21	M	III	YLD-MOIST-KWT-KQUAL	KH-LYS	42-17	3.25	4.22

Table 46. Weights of indices listed in Table 45, with weights of corresponding pure S_2 indices for comparison purposes

Index no.	Restrictions[a]	Type	Weights										
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
45-1	MP	I	1		.94	-27				49.9[b]		-2.0[b]	
45-12	M	I	1		.05	-29				33.2[b]		-1.5[b]	
38-10	MP	I	1		.94	-27				49.9[b]		-2.0	
45-2		I	1	-1.1	3.06	-59				76.7[b]		-2.4[b]	
45-13	M	I	1	-1.2	16.2	-393				193[b]		-2.2[b]	
42-6	MP	I	1	-.8	2.62	-50				71.8[b]		-2.4	
45-3	MP	I	1		.94	-27				49.9[b]	1.9[b]	-2.0[b]	
45-14	MP	I	1		.29	-93				57.9[b]	-749[b]	-2.6[b]	
42-8	MP	I	1		1.02	-19				48.9	93.2	-1.9	
45-4	M	II	1		2.82			-22[b]	879[b]			-1.8[b]	
45-15	M	II	1		2.10			-16[b]	726[b]			-1.4[b]	
38-14		II	1		1.24			-19[b]	664[b]			-1.9	
45-5	M	II	1		3.05			-20[b]	939[b]		126[b]	-1.8[b]	
45-16	M	II	1		4.12			5.1[b]	1263[b]		1092[b]	-1.4[b]	
42-12		II	1		1.57			-15[b]	883[b]		-479	-2.3	
45-6	MP	II	1	.5	1.41			-21[b]	681[b]			-1.8[b]	
45-17	M	II	1	-.6	3.51			-13[b]	888[b]			-1.2[b]	
42-10	M	II	1	.5	1.10			-19	630			-1.7	
45-7	M	III	1	-.4	1.53				512[b]			-.5[b]	
45-18	M	III	1	-.7	2.13				590[b]			-.5[b]	
38-25	M	III	1	-.2	.85				423[b]			-.6	
45-8	M	III	1	-1.2	1.92				732[b]				-24
38-26	M	III	1	-.9	.96				629				-27

[a] See Table 45 for description of restrictions.

[b] Trait measured on S_1 plant basis.

Table 46 (Continued)

Index no.	Restrictions[a]	Type	Weights									
			YLD	MOIST	KWT	ER	KH	PROT	LYS	LP	HIST	OPAC	KQUAL
45-9	M	III	1	-.7	1.39		1.3[b]		460[b]				
45-19	M	III	1	-1.0	2.36		1.1[b]		591[b]				
38-23	M	III	1	-.5	.88		1.4		390[b]				
45-10	M	III	1	-.5	1.46				537[b]			-.4[b]	-4.8
45-20	M	III	1	-.7	1.57				595[b]			-.3[b]	-11
42-20	M	III	1	-.3	.74				447[b]			-.5	-5.4
45-11	M	III	1	-.8	1.42		.7[b]		555[b]				-11
45-21	M	III	1	-1.3	2.08		-.3[b]		794				-29
42-17	M	III	1	-.7	.75		.6		507				-16

Table 47. Expected gains per cycle in YLD for restricted[a] selection indices incorporating S_1 plant and S_2 progeny data[b] when culling of S_1 plants is practiced

Index no.	Type	r[d]	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
Only protein traits on S_1 plants											
45-1	I	-.37	.0	100	5.91	5.2	105	6.04	77.9	452	8.95
45-2	I	-.29	.0	100	6.28	2.3	102	6.32	81.1	500	9.64
45-3	I	-.37	.0	100	5.91	5.2	106	6.04	77.8	450	8.95
45-4	II	-.35	11.5	113	4.42	28.9	141	4.75	69.8	331	5.98
45-5	II	-.34	10.5	112	4.40	27.8	139	4.76	69.9	333	6.00
45-6	II	-.43	15.4	118	4.80	32.7	149	5.19	69.5	328	6.28
45-7	III	-.25	32.2	147	3.78	46.2	186	4.07	69.7	330	4.68
45-8	III	-.22	28.9	141	3.67	43.7	178	3.95	69.5	328	4.60
45-9	III	-.46	29.1	141	3.65	43.9	178	3.92	69.5	328	4.57
45-10	III	-.24	33.0	149	3.81	46.7	188	4.09	69.8	331	4.70
45-11	III	-.21	30.9	145	3.74	45.2	183	3.99	69.6	329	4.62

[a] See Table 42 for restrictions.

[b] S_2 progeny data from two locations with two replications per location.

[c] Protection level (probability that a single plant for which the value of the S_1 portion of the index falls at the point separating selections from discards would produce an S_2 progeny for which the value of the S_2 portion of the index was so high that the family fell into the selected class, based on the total index).

[d] Phenotypic correlation between S_1 plant and S_2 progeny portions of the index.

[e] Percentage of single plants that could be culled based on the given protection level and a 20% selection intensity in the S_2 testing stage.

[f] Number of S_1 plants to be measured if it is desired to test 100 S_2 progenies; maximum of 500 single plants permitted.

[g] Based on selection of 20 families using the total index.

Table 47 (Continued)

Index no.	Type	r[d]	Protection Level[c] 5%			10%			25%		
			% culling[e]	Plants tested[f]	Gain q/ha[g]	% culling	Plants tested	Gain q/ha	% culling	Plants tested	Gain q/ha
Protein and other traits on S_1 plants											
45-12	I	.00	38.3	162	4.40	50.5	202	4.66	70.3	336	5.27
45-13	I	-.36	17.4	121	4.29	34.6	153	4.63	69.4	327	5.66
45-14	I	-.24	30.9	145	3.98	45.2	182	4.25	69.6	329	4.92
45-15	II	-.24	33.6	151	3.74	47.2	189	3.99	69.8	331	4.59
45-16	II	-.28	16.8	120	3.95	34.0	152	4.27	69.4	327	5.22
45-17	II	-.26	16.6	120	3.70	33.9	151	3.99	69.4	327	4.88
45-18	II	-.24	25.6	134	3.62	41.2	170	3.90	69.4	327	4.60
45-19	II	-.19	26.3	136	3.47	41.8	172	3.73	69.4	327	4.40
45-20	II	-.24	30.2	143	3.76	44.7	181	4.04	69.6	329	4.68
45-21	III	-.22	27.8	139	3.67	43.0	175	3.92	69.5	327	4.60

A cost of 20 to 30% of the genetic gain from use of a type II or III index was incurred when protein traits were measured in the earlier generation. Transferring the determination of KH or OPAC to the S_1 generation as well had little additional effect on gain.

As with S_1 and full-sib indices, the use of single plant data with S_2 indices usually produced larger weights on MOIST, KWT, and LYS in relation to YLD (Table 46). Severe shifts in weights were noted in a few cases (e.g., 45-13).

The correlations between the S_1 and S_2 portions of the S_2-S_1 index were generally more negative than those encountered in connection with S_1 or full-sib testing (Table 47). For a given protection level, the culling percentages permitted by S_2-S_1 indices were slightly lower than those permitted by their S_1-S_0 counterparts. As with S_1-S_0 and full-sib single plants indices, most indices were clustered about the 70% culling level when the protection level was 25%.

CONCLUSIONS AND SUMMARY

The choice of a selection index does not depend solely on expected gain. Other factors that should be considered are the degree to which biased or imprecise estimates of the population parameters affect gain and the expense and labor involved in collecting the necessary data.

Division of selection indices into types (I, II, III, IV) was justified by the above considerations. Type I indices had the highest expected gains, but the weights of such indices accorded a disproportionate importance to ER, an indication that the gain was largely dependent on correlated changes in YLD, KH, and LP that were expected to occur on selection for ER. Weights on YLD were negative for a few type I indices. Further, since there is much season-to-season variability in the degree to which ear rot is expressed in opaque-2 maize, and since the correlations involving ER obtained in this study were not consistent with those reported by other researchers, it is concluded that use of an index with such weights would entail excessive risk.

Type II indices represented an attempt to use correlated characters (HIST, PROT) to supplement the primary protein traits (LYS, LP) or to use both LYS and LP to characterize protein quality. The weights of type II

indices, however, imposed highly antagonistic selection on combinations of protein traits. Poor agreement between expected and realized response to antagonistic selection has been reported frequently (Bohren et al., 1966; Rutledge et al., 1973; Moll et al., 1975). If a type II index were applied, the consequence of divergence of the actual from the predicted response would be failure to achieve the selection goals. In addition, the success of a type II index is dependent on precise, unbiased estimates of the covariances among protein traits.

Type III indices, which included only one of the protein characters and excluded ER, were lower in expected gain than indices of types I and II but had weights suggestive of a lesser degree of reliance on correlated responses. As a consequence, type III indices would probably give satisfactory gains even if the parameters had been estimated poorly or changed by selection. Among type III indices, the five-trait combinations seemed to be most efficient. The addition of a sixth trait contributed little to expected gain. The most effective five-trait index in each of the three breeding schemes was the one incorporating YLD, MOIST, KWT, LYS, and OPAC (index 17-89 for S_1 testing, 28-43 for full-sib testing, and 38-25 for S_2 testing). Weights of these indices assigned high importance (relative to YLD) to LYS, with KWT approximately equal to YLD and MOIST and OPAC

of lesser importance. The four-trait index incorporating YLD, KWT, LYS, and OPAC, but not MOIST (index 14-93) produced expected gains only 7% smaller than index 17-89, but MOIST is relatively easy to determine and can be incorporated into the index with little additional effort. The five-trait index incorporating YLD, MOIST, KWT, KH, and LYS (index 17-90 for S_1 testing, 28-41 for full-sib testing, and 38-23 for S_2 testing) produced slightly smaller expected gains than YLD, MOIST, KWT, LYS and OPAC but would perhaps be more desirable in that gain in KH would be achieved by direct selection rather than as a correlated response to selection for OPAC.

As cycles of selection are carried out and new estimates of parameters become available, the "optimum" weights and the "optimum" set of traits to include in an index may change. Strictly, the results presented here pertain only to the population BSAAo_2(S)C1 (although some individual plant data came from BSAAo_2(S)C2. Since, however, the parameter estimates determined for this population were similar to those reported in other opaque-2 populations, the conclusions of this study may have more general utility.

Table 48 summarizes the expected gain per year from the most effective type III index (of five or six traits) in each breeding scheme. The S_1 testing scheme that completed a cycle in two years was superior to the other schemes.

Table 48. Expected gain per year in YLD for the most effective five- or six-trait restricted[a] indices of type III for S_1, full-sib, and S_2 testing with and without use of individual plant data

Breeding scheme	Expected Gain per Year in YLD (q/ha)				
	All data[b] from progeny trials	Individual plant data[c]			
		No culling	PL[d]=5%	PL=10%	PL=25%
S_1 testing (3 years/cycle)	1.14 (20-43)[e]	.81 (25-9)	.93 (25-9)	1.00 (25-22)	1.15 (25-9)
S_1 testing (2 years/cycle)	1.71 (20-43)	1.63 (25-32)	1.63 (25-32)	1.63 (25-32)	2.50 (25-32)
Full-sib testing (2 years/cycle)	1.04 (28-43)	.64 (35-19)	.76 (35-21)	.81 (35-21)	.91 (35-21)
S_2 testing (4 years/cycle)	1.12 (42-20)	.83 (45-7)	.95 (45-10)	1.02 (45-10)	1.18 (45-10)

[a] The restriction that gains in YLD, KH, and LP be in the ratio 200:24:1 was used in all indices; restrictions that MOIST or PROT remain unchanged were used when otherwise MOIST would increase or PROT decrease.

[b] Data from two locations with two replications per location for all traits.

[c] Individual plant data in place of progeny data for OPAC (S_1 testing, 2 years/cycle) or for protein traits (other breeding schemes).

[d] Protection level (probability that an individual plant for which the value of the individual plant portion of the index falls at the point separating selections from discards would produce a progeny for which the value of the progeny portion of the index was so high that the family fell into the selected class based on the total index).

[e] Number of index.

Substitution of single-plant data for replicated progeny data caused reductions in expected gain that could not be recovered by culling of individual plants at the 5 and 10% protection levels. The expected gains for culling at the 25% protection level were undoubtedly biased upward.

The use of individual S_0 data has advantages and disadvantages that are not reflected in expected gains. One advantage is the need for fewer protein determinations. A single determination would be made for each plant, rather than a determination for each family in each replication. (Reduction in the number of determinations needed in the progeny tests could be achieved, however, by using a composite sample, made up of equal amounts of seed from each replication, for each family.)

Among the disadvantages are:

1) Environmental effects in the breeding nursery may differ from those in the testing site. Nursery seed results from hand-pollination which may affect some characters. Also, genotype x environment interaction may be important for seed produced in a winter nursery.

2) The ability to update the index would be hampered by difficulties in estimating the complete set of parameters. In particular, the genetic variances and covariances among traits measured on individual plants could not be estimated. If culling based on individual plant data were carried out

there would be the additional complication that complete data would be available for the selected lines only and not the full random sample of genotypes. The consequences of using parameter estimates derived from selected rather than random populations are uncertain.

3) In this study, transferring the determination of protein traits to the generation preceding progeny testing was accompanied by shifts of the index weights. With type III indices, heavier weights were given to KWT, MOIST, and LYS in relation to YLD. This indicates greater dependence on correlated responses for improvement in YLD.

4) Procedures for determining the optimum protection level have not been developed.

5) In this study, all individual plant data came from experiments (77107, 78105) in which the presence of ear rot necessitated the use of a selected, rather than a truly random sample in estimating parameters. Thus, phenotypic variances on an individual plant basis have probably been underestimated, resulting in an overestimate of the expected gain when individual plant data are used in an index.

Further study of this subject would be useful in clarifying the risks and benefits of using individual plant data. However, on the basis of this study, the use of individual plant data does not appear to be warranted.

Following is a summary of the results of this study:

1) Estimates of variances and covariances for traits important in breeding opaque-2 maize were presented. With few exceptions, these estimates were consistent with those reported in other experiments with opaque-2 maize.

2) Phenotypic variances and covariances on a single plant basis were obtained for protein and kernel quality characters.

3) Selection indices incorporating different combinations of traits were calculated for three recurrent selection schemes (S_1, full-sib, and S_2 testing). Selection goals were defined by specifying grain yield (YLD) as the only character bearing economic value and by using restrictions to require genetic gain in kernel hardness (KH) and g lysine/100 g protein (LP). Restrictions were also used where necessary to avoid an increase in grain moisture content at harvest (MOIST) or a decrease in grain protein content (PROT). Though arbitrary, the selection goals for KH and LP could be altered within reasonable limits without significantly affecting the ranking of combinations of traits for effectiveness in selection indices.

4) Though they did not produce the highest expected gains, indices of type III, i.e., those that excluded ear rot resistance score (ER) and included only one of the protein traits (PROT, LP, lysine content (LYS), and histidine content (HIST)), were recommended because they were expected

to be less dependent than other types of indices on the quality of the parameter estimates.

5) Substitution of single plant data for data from replicated progeny tests was considered in connection with each breeding scheme. The possibility of increasing the effective selection intensity, given that resources for replicated testing were fixed, by culling individual plants was investigated, but the disadvantages of utilizing single plant data appeared to outweigh the advantages.

6) Among type III indices, those that incorporated five traits were most efficient. The addition of a sixth trait contributed very little to expected gains.

7) The most effective combinations for S_1 testing were also the most effective for full-sib testing and S_2 testing.

8) The most important traits with respect to achieving the specified selection goals were YLD, MOIST, KH, LYS, kernel weight, and degree of light transmission by kernels. Selection for ear rot resistance would be desirable when possible, but ER was of doubtful value as a character in a selection index.

9) Sampling standard deviations of expected gains from direct selection and index selection were large and were of little value in selecting among indices. Bias, rather than lack of precision, may be the primary factor limiting

the ability to predict gains associated with the application of a selection index.

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APPENDIX A: CALCULATION OF THE SAMPLING VARIANCE OF THE EXPECTED GAIN FROM SELECTION

The basis for the calculation of the sampling variance of the expected gain was the formulation utilized by Mode and Robinson (1959). If a statistic, $\phi(m_1,m_2,\ldots,m_k)$ is a function of moments $m_1,m_2,\ldots,m_k$, then, approximately,

$$\mathrm{Var}(\phi) = \sum_i \left(\frac{\partial\phi}{\partial m_i}\right)^2 \mathrm{Var}(m_i) + \sum_{i\neq j} \frac{\partial\phi}{\partial m_i}\frac{\partial\phi}{\partial m_j}\mathrm{Cov}(m_i,m_j). \qquad (A1)$$

The following development is specialized in that it applies to the prediction of gains from S_1 progeny selection (without use of S_0 data) from parameters derived from a design II experiment. To simplify calculations it has been assumed that the number of locations and replications used in the design II experiment and in the testing phase of the selection program were the same.

The sampling variance was calculated without regard for the dependence of index weights on the parameter estimates. The variance, therefore, represents the variability in response expected if a particular index were applied to a series of replicates of the population.

The expected gain in trait x_i on selection in an index I is given by

$$\Delta g_i = k_s \frac{s_{A;Ii}}{s_{P;I}}$$

where k_s is the standardized selection differential, $s_{A;Ii}$ the genetic covariance between I and x_i, and $s_{P;I}$ the phenotypic variance in I.

For S_1 testing this becomes, in terms of the variance and covariance components from the design II experiment,

$$\Delta g_i = \frac{2k_s(s_{M;Ii}+s_{F;Ii})}{\sqrt{2(s^2_{M;I}+s^2_{F;I})+s^2_{MF;I}+[2(s^2_{ML;I}+s^2_{FL;I})+s^2_{MFL;I}]/\ell + s^2_{e;I}/r\ell}}$$

where

$s_{M;Ii} = S_1$ = male component of covariance of I and i;

$s_{F;Ii} = S_2$ = female component of covariance of I and i;

$s^2_{M;I} = S_3$ = male component of variance for I;

$s^2_{F;I} = S_4$ = female component of variance for I;

$s^2_{MF;I} = S_5$ = male x female component of variance for I;

$s^2_{ML;I} = S_6$ = male x location component of variance for I;

$s^2_{FL;I} = S_7$ = female x location component of variance for I;

$s^2_{MFL;I} = S_8$ = male x female x location component of variance for I;

and

$s^2_{e;I} = S_9$ = error component of variance I.

For convenience, let $N = 2k_s(s_{M;Ii} + s_{F;Ii})$ and

$$D = 2(s^2_{M;I}+s^2_{F;I}) + s^2_{MF;I} + [2(s^2_{ML;I}+s^2_{FL;I}) + s^2_{MFL;I}]/\ell + s^2_{e;I}/r\ell$$

so that

$$\Delta g_i = ND^{-1/2}.$$

Now Δg_i has been written as a function of the nine moments $S_1, S_2, \ldots, S_9$, so that expression (A1) applies. The result is an expression containing 45 terms, as follows:

$$\begin{aligned}
\mathrm{Var}(g_i) = {} & \frac{4k_s^2}{D}\mathrm{Var}(S_1) + \frac{4k_s^2}{D}\mathrm{Var}(S_2) + \frac{N^2}{D^3}\mathrm{Var}(S_3) + \frac{N^2}{D^3}\mathrm{Var}(S_4) \\
& + \frac{N^2}{4D^3}\mathrm{Var}(S_5) + \frac{N^2}{\ell^2 D^3}\mathrm{Var}(S_6) + \frac{N^2}{\ell^2 D^3}\mathrm{Var}(S_7) + \frac{N^2}{4\ell^2 D^3}\mathrm{Var}(S_8) \\
& + \frac{N^2}{4r^2\ell^2 D^3}\mathrm{Var}(S_9) + \frac{8k_s^2}{D}\mathrm{Cov}(S_1,S_2) - \frac{4Nk_s}{D^2}\mathrm{Cov}(S_1,S_3) \\
& - \frac{4Nk_s}{D^2}\mathrm{Cov}(S_1,S_4) - \frac{Nk_s}{D^2}\mathrm{Cov}(S_1,S_5) - \frac{4Nk_s}{\ell D^2}\mathrm{Cov}(S_1,S_6) \\
& - \frac{4Nk_s}{\ell D^2}\mathrm{Cov}(S_1,S_7) - \frac{2Nk_s}{\ell D^2}\mathrm{Cov}(S_1,S_8) - \frac{2Nk_s}{r\ell D^2}\mathrm{Cov}(S_1,S_9) \\
& - \frac{4Nk_s}{D^2}\mathrm{Cov}(S_2,S_3) - \frac{4Nk_s}{D^2}\mathrm{Cov}(S_2,S_4) \\
& - \frac{2Nk_s}{D^2}\mathrm{Cov}(S_2,S_5) - \frac{4Nk_s}{\ell D^2}\mathrm{Cov}(S_2,S_6) - \frac{4Nk_s}{\ell D^2}\mathrm{Cov}(S_2,S_7) \\
& - \frac{2Nk_s}{\ell D^2}\mathrm{Cov}(S_2,S_8) - \frac{2Nk_s}{r\ell D^2}\mathrm{Cov}(S_2,S_9) + \frac{2N^2}{D^3}\mathrm{Cov}(S_3,S_4) \\
& + \frac{N^2}{D^3}\mathrm{Cov}(S_3,S_5) + \frac{2N^2}{\ell D^3}\mathrm{Cov}(S_3,S_6) + \frac{2N^2}{\ell D^3}\mathrm{Cov}(S_3,S_7) \\
& + \frac{N^2}{\ell D^3}\mathrm{Cov}(S_3,S_8) + \frac{N^2}{r\ell D^3}\mathrm{Cov}(S_3,S_9) + \frac{N^2}{D^3}\mathrm{Cov}(S_4,S_5)
\end{aligned}$$

$$+ \frac{2N^2}{\ell D^3} \mathrm{Cov}(S_4,S_6) + \frac{2N^2}{\ell D^3} \mathrm{Cov}(S_4,S_7) + \frac{N^2}{\ell D^3} \mathrm{Cov}(S_4,S_8)$$

$$+ \frac{N^2}{r\ell D^3} \mathrm{Cov}(S_4,S_9) + \frac{N^2}{\ell D^3} \mathrm{Cov}(S_5,S_6) + \frac{N^2}{\ell D^3} \mathrm{Cov}(S_5,S_7)$$

$$+ \frac{N^2}{2\ell D^3} \mathrm{Cov}(S_5,S_8) + \frac{N^2}{2r\ell D^3} \mathrm{Cov}(S_5,S_9) + \frac{2N^2}{\ell^2 D^3} \mathrm{Cov}(S_6,S_7)$$

$$+ \frac{N^2}{\ell^2 D^3} \mathrm{Cov}(S_6,S_8) + \frac{N^2}{r\ell^2 D^3} \mathrm{Cov}(S_6,S_9) + \frac{N^2}{\ell^2 D^3} \mathrm{Cov}(S_7,S_8)$$

$$+ \frac{N^2}{r^2\ell^2 D^3} \mathrm{Cov}(S_7,S_9) + \frac{N^2}{2r\ell^2 D^3} \mathrm{Cov}(S_8,S_9) \qquad \text{(A2)}$$

Each of the terms $\mathrm{Var}(S_j)$ and $\mathrm{Cov}(S_j,S_k)$ of (A2) is then expanded and the variance and covariance components expressed in terms of mean squares from the design II analysis of variance. For example, the first term

$$\mathrm{Var}(S_1) = \mathrm{Var}(s_{M;Ii})$$

$$= \mathrm{Var}(b_1 s_{M;1i} + b_2 s_{M;2i} + \ldots + b_n s_{M;ni}),$$

where

$$I = b_1 x_1 + b_2 x_2 + \ldots + b_n x_n,$$

and

$s_{M;ji}$ = male component of $\mathrm{Cov}(x_j,x_i)$ (a variance if $j = i$).

Expanding further,

$$\text{Var}(S_1) = \text{Var}[b_i s^2_{M;i} + \sum_{j\neq i} b_j s_{M;ji}]$$

$$= b_i^2 \text{ Var}(s^2_{M;i}) + \sum_{j\neq i} [b_j^2 \text{ Var}(s_{M;ji})]$$

$$+ 2 \sum_{j\neq i} b_i b_j \text{ Cov}(s^2_{M;i}, s^2_{M;ji})$$

$$+ 2 \sum_{\substack{k>j \\ k\neq i}} \sum_{j\neq i} b_j b_k \text{ Cov}(s_{M;ji}, s_{M;ki}). \qquad \text{(A3)}$$

In terms of mean squares and mean products,

$$s^2_{M;i} = \frac{1}{rm\ell} (M_{M;i} - M_{MF;i} - M_{ML;i} + M_{MFL;i}),$$

and

$$s_{M;ji} = \frac{1}{rm\ell}(M_{M;ji} - M_{MF;ji} - M_{ML;ji} + M_{MFL;ji})$$

where r = number of replications per location, ℓ = number of locations, m = number of males per set and f = number of females per set.

Mean squares for M_M, M_{MF}, M_{ML}, and M_{MFL} are independent so (A3) becomes

$$\text{Var}(S_1) = \frac{b_i^2}{r^2 m^2 \ell^2} [\text{Var}(M_{M;i}) + \text{Var}(M_{MF;i}) + \text{Var}(M_{ML;i})$$

$$+ \text{Var}(M_{MFL;i})]$$

$$+ \frac{1}{r^2 m^2 \ell^2} \sum_{j\neq i} b_j^2 [\text{Var}(M_{M;ji}) + \text{Var}(M_{MF;ji})$$

$$+ \text{Var}(M_{ML;ji}) + \text{Var}(M_{MFL;ji})]$$

$$+ \frac{2}{r^2 m^2 \ell^2} \sum_{j \neq i} b_i b_i [\mathrm{Cov}(M_{M;i}, M_{M;ij}) + \mathrm{Cov}(M_{MF;i}, M_{MF;ij})$$

$$+ \mathrm{Cov}(M_{ML;i}, M_{ML;ij}) + \mathrm{Cov}(M_{MFL;i}, M_{MFL;ij})]$$

$$+ \frac{2}{r^2 m^2 \ell^2} \sum_{\substack{k>j \\ k \neq i}} \sum_{j=i} b_j b_k [\mathrm{Cov}(M_{M;ji}, M_{M;ki}) + \mathrm{Cov}(M_{MF;ji}, M_{MF;ki})$$

$$+ \mathrm{Cov}(M_{ML;ji}, M_{ML;ki}) + \mathrm{Cov}(M_{MFL;ji}, M_{MFL;ki})].$$

Finally, estimates of variances and covariances of mean squares and mean products are obtained as indicated by Mode and Robinson (1959): let a_{ij} and $a_{k\ell}$ be any mean squares (if i=j and k=ℓ) or mean products and let s_{ij} and $s_{k\ell}$ be the sample estimates for a_{ij} and $a_{k\ell}$, respectively, with P degrees of freedom. Then

$$\mathrm{Cov}(a_{ij}, a_{k\ell}) \doteq \frac{s_{ik}s_{j\ell} + s_{i\ell}s_{jk}}{P+2} .$$

This expression is also applied to calculate variances, so that, for example

$$\mathrm{Var}(a_{ii}) \doteq \frac{2s_{ii}^2}{P+2} .$$

With P_M, P_{MF}, P_{ML}, and P_{MFL} equal, respectively, to the degrees of freedom for males/sets, males x females/sets, males x locations/sets, and males x females x locations/sets, (A3) becomes:

$$\mathrm{Var}(S_1) \doteq \frac{1}{r^2 m^2 \ell^2}\Big[b_i^2\Big(\frac{2M_{M;i}^{\,2}}{P_M+2} + \frac{2M_{MF;i}^{\,2}}{P_{MF}+2} + \frac{2M_{ML;i}^{\,2}}{P_{ML}+2} + \frac{2M_{MFL;i}^{\,2}}{P_{MFL}+2}\Big)$$

$$+ \sum_{j\neq i} b_j^2\Big(\frac{M_{M;i}M_{M;j}+M_{M;ij}^{\,2}}{P_M+2} + \frac{M_{MF;i}M_{MF;j}+M_{MF;ji}^{\,2}}{P_{MF}+2}$$

$$+ \frac{M_{ML;i}M_{ML;j}+M_{ML;ji}^{\,2}}{P_{ML}+2} + \frac{M_{MFL;i}M_{MFL;j}+M_{MFL;ij}^{\,2}}{P_{MFL}+2}\Big)$$

$$+ 2\sum_{j\neq i} b_i b_j\Big[\frac{2M_{M;i}M_{M;ij}}{P_M+2} + \frac{2M_{MF;i}M_{MF;ij}}{P_{MF}+2}$$

$$+ \frac{2M_{ML;i}M_{ML;ij}}{P_{ML}+2} + \frac{2M_{MFL;i}M_{MFL;ij}}{P_{MFL}+2}\Big)$$

$$+ 2\sum_{\substack{k>j\\k\neq i}}\sum_{j\neq i} b_j b_k\Big(\frac{M_{M;ji}M_{M;ki}+M_{M;i}M_{M;jk}}{P_M+2}$$

$$+ \frac{M_{MF;ji}M_{MF;ki}+M_{MF;i}M_{MF;jk}}{P_{MF}+2}$$

$$+ \frac{M_{ML;ji}M_{ML;ki}+M_{ML;i}M_{ML;jk}}{P_{ML}+2}$$

$$+ \frac{M_{MFL;ji}M_{MFL;ki}+M_{MFL;i}M_{MFL;jk}}{P_{MFL}+2}\Big)\Big]$$

APPENDIX B: CALCULATION OF COVARIANCES BETWEEN SINGLE-PLANT TRAITS AND PROGENY TRAITS

The calculation of the covariance between trait X, measured on an individual plant, and trait Y, measured as a progeny mean, is here determined for the three cases

1) $Cov(X_{S_0}, Y_{S_1})$, where X is measured on an S_0 plant and Y on the S_1 progeny;

2) $Cov(X_{S_0}, Y_{FS})$, where X is measured on an S_0 plant and Y on the full-sib progeny;

and

3) $Cov(X_{S_1}, Y_{S_2})$, where X is measured on an S_1 plant and Y on the S_2 progeny.

It is assumed that linkage and epistasis are absent, so that the contribution of a given locus (with two alleles B and b) can be considered independently of other loci.

The frequences and genotypic values are denoted as follows:

genotype	frequency		value	
	S_0	S_1	X	Y
BB	p^2	$p^2 + \frac{1}{2}pq$	a_X	a_Y
Bb	$2pq$	pq	d_X	d_Y
bb	q^2	$q^2 + \frac{1}{2}pq$	$-a_X$	$-a_Y$

The means in X of the S_0, S_1, and S_2 generations are given by

$$\mu_{(S_0)X} = (p - q)a_X + 2pqd_X,$$

$$\mu_{(S_1)X} = (p - q)a_X + pqd_X,$$

$$\mu_{(S_2)X} = (p - q)a_X + \tfrac{1}{2}pqd_X,$$

and similarly for means in Y. the mean value in Y of the selfed progeny of a Bb plant is $\frac{1}{2}d_Y$.

The additive and dominance components of covariance were given (in different notation) by Mode and Robinson (1959):

$$\sigma_{A;XY} = 2pq[a_X + d_X(q-p)][a_Y + d_Y(q-p)],$$

and

$$\sigma_{D;XY} = 4p^2q^2d_Xd_Y.$$

Now,

$$\begin{aligned}\mathrm{Cov}(X_{S_0},Y_{S_1}) &= p^2a_Xa_Y + pqd_Xd_Y + q^2a_Xa_Y \\ &\quad - [(p-q)a_X + 2pqd_X][(p-q)a_Y + pqd_Y] \\ &= 2pqa_Xa_Y + pq(p^2+q^2)d_Xd_Y + 2pq(q-p)a_Yd_X \\ &\quad + pq(q-p)a_Xd_Y \\ &= \sigma_{A;XY} + \tfrac{1}{2}\sigma_{D;XY} - pq(q-p)d_Y[a_X+d_X(q-p)].\end{aligned}$$

If the last term is assumed to be 0 (i.e., if $p = q = \frac{1}{2}$ or $d_Y = 0$), then $\mathrm{Cov}(X_{S_0},Y_{S_1}) = \sigma_{A;XY} + \frac{1}{2}\sigma_{D;XY}$.

Similarly,

$$\begin{aligned}\mathrm{Cov}(X_{S_1}, Y_{S_2}) &= (p^2+\tfrac{1}{2}pq)a_X a_Y + \tfrac{1}{2}pqd_X d_Y + (q^2+\tfrac{1}{2}pq)a_X a_Y \\ &\quad - [(p-q)a_X + pqd_X][(p-q)a_Y + \tfrac{1}{2}pqd_Y] \\ &= 3pqa_X a_Y + pq(q-p)a_Y d_X + \tfrac{1}{2}pq(q-p)a_X d_Y \\ &\quad + \tfrac{1}{2}pq(1-pq)d_X d_Y \\ &= \tfrac{3}{2}\sigma_{A;XY} + \tfrac{3}{8}\sigma_{D;XY} \\ &\quad - \tfrac{1}{2}pq(q-p)[4a_Y d_X + 5a_X d_Y + 5(q-p)d_X d_Y].\end{aligned}$$

If $p = q = \frac{1}{2}$, $\mathrm{Cov}(X_{S_1}, Y_{S_2}) = \frac{3}{2}\sigma_{A;XY} + \frac{3}{8}\sigma_{D;XY}$.

If full-sib progenies are produced by plant-to-plant matings, the following possibilities may occur:

female	male	frequency of mating	female mean in X	progeny mean in Y
BB	BB	p^4	a_X	a_Y
BB	Bb	$2p^3q$	a_X	$\frac{1}{2}(a_Y+d_Y)$
BB	bb	p^2q^2	a_X	d_Y
Bb	BB	$2p^3q$	d_X	$\frac{1}{2}(a_Y+d_Y)$
Bb	Bb	$4p^2q^2$	d_X	$\frac{1}{2}d_Y$
Bb	bb	$2pq^3$	d_X	$\frac{1}{2}(-a_Y+d_Y)$
bb	BB	p^2q^2	$-a_X$	d_Y
bb	Bb	$2pq^3$	$-a_X$	$\frac{1}{2}(-a_Y+D_Y)$
bb	bb	q^4	$-a_X$	$-a_Y$

The mean in Y is $\mu_Y = (p-q)a_Y + 2pqd_Y$.

Now,

$$\begin{aligned}
\mathrm{Cov}(X_{S_0}, Y_{FS}) &= p^4 a_X a_Y + p^3 q a_X (a_Y + d_Y) + p^2 q^2 a_X d_Y \\
&\quad + p^3 q (a_Y + d_Y) d_X + 2p^2 q^2 d_X d_Y + p q^3 d_X (d_Y - d_Y) - p^2 q^2 a_X d_Y \\
&\quad - p q^3 a_X (d_Y - a_Y) + q^4 a_X a_Y - [(p-q)a_X \\
&\quad + 2pqd_X][(p-q)a_Y + 2pqd_Y] \\
&= pq[a_X a_Y + (q-p)a_X d_Y + (q-p)a_Y d_X \\
&\quad + (q-p)^2 d_X d_Y] \\
&= \tfrac{1}{2}\sigma_{A;XY}.
\end{aligned}$$

APPENDIX C: VARIANCE COMPONENT ESTIMATES USED IN CALCULATING SELECTION INDICES

Table 49. Estimates of additive (A), additive x location (AL), dominance (D), dominance x location (DL), and error (E) components of variance and covariance for seventeen traits measured in the design II experiment, with variance components on the diagonal

	YLD	MOIST	KWT	SPGRAV	ER	KH	PROT	LYS	LP
A YLD	36.30								
AL	20.33								
D	43.67								
DL	0.00[a]								
E	60.65								
A MOIST	-3.22	7.809							
AL	-1.93	.285							
D	-4.51	2.522							
DL	1.50	1.404							
E	-2.10	1.696							
A KWT	18.37	2.46	65.47						
AL	-.64	.23	.50						
D	-8.34	-1.71	7.50						
DL	5.29	-2.48	.27						
E	6.52	.86	20.75						
A SPGRAV	-.0152	.0065	.0077	.313[b]					
AL	-.0347	-.0065	-.0194	.000[a]					
D	-.0743	-.0054	-.0377	.047[b]					
DL	.0614	.0248	.0248	.668[b]					
E	.0315	.0004	.0263	2.206[b]					
A ER	-1.190	-.200	.444	.18[b]	.231				
AL	.243	-.027	-.033	-.84[b]	.009				
D	-.245	-.447	.236	-3.07[b]	.150				
DL	-.536	-.016	.103	2.06[b]	.049				
E	-.214	.056	-.008	-.99[b]	.188				

[a]Value of 0 used in place of a negative estimate.

[b]Multiply value in Table by 10^{-3} to obtain correct value.

Table 49 (Continued)

	YLD	MOIST	KWT	SPGRAV	ER	KH	PROT	LYS	LP	HIST	HP
A KH	-3.974	2.419	2.54	8.00[b]	-.310	3.68					
AL	.382	-.204	.91	13.06[b]	.122	1.27					
D	.258	-.004	-.30	11.99[b]	-.077	1.67					
DL	-.433	.889	-3.07	.26[b]	-.156	.00[a]					
E	-.531	.171	.54	-1.55[b]	-.030	5.62					
A PROT	-1.072	.446	-.610	-.88[b]	-.0786	.551	.297				
AL	-.035	-.005	-.206	1.36[b]	.0083	.199	.009				
D	.260	.025	-.554	2.77[b]	-.0256	.072	.114				
DL	-.788	-.147	-.065	-5.40[b]	.0114	-.252	.000[a]				
E	-.190	-.024	.128	-.72[b]	.0188	.188	.242				
A LYS	-.0406	.0044	-.0479	-.189[b]	3.70[b]	4.86[b]	10.24[b]	.564[b]			
AL	-.0272	.0033	-.0103	.007[b]	.12[b]	6.60[b]	.38[b]	.074[b]			
D	-.0145	.0010	-.0383	-.103[b]	2.96[b]	-2.35[b]	3.40[b]	.278[b]			
DL	.0046	-.0118	.0372	-.016[b]	-2.52[b]	-3.08[b]	1.74[b]	.141[b]			
E	-.0020	-.0009	.0049	.004[b]	.85	4.73[b]	5.55[b]	.627[b]			
A LP	-.0137	-.1418	-.244	-1.67[b]	-.0020	-.2464	-.0299	1.69[b]	.0364		
AL	-.1949	.0447	-.029	-.82[b]	-.0009	.0036	-.0077	.02[b]	.0031		
D	-.4627	-.0082	-.165	-.65[b]	.0466	-.0705	-.0264	1.43[b]	.0263		
DL	.5552	-.0398	.474	3.58[b]	-.0360	.0492	.0390	.70[b]	.0009		
E	.0865	-.0027	.002	-.25[b]	-.0002	-.0235	-.0576	4.39[b]	.0802		
A HIST	-.0407	.0152	-.015	-.094[b]	-.73[b]	.0136	7.62[b]	.296[b]	-.37[b]	.242[b]	
AL	-.0145	.0014	-.007	.036[b]	-.22[b]	.0017	.03[b]	.013[b]	.09[b]	.008[b]	
D	-.0082	-.0005	-.006	-.009[b]	.80[b]	.0023	1.48[b]	.116[b]	.54[b]	.053[b]	
DL	-.0070	-.0040	.014	-.030[b]	-1.42[b]	-.0032	1.22[b]	.068[b]	-.02[b]	.040[b]	
E	-.0016	-.0003	-.001	.002	.58	.0063	3.55	.317	1.93	.251[b]	
A HP	-.164	.077	-.005	-.84[b]	.0116	-.0281	-.0073	.15[b]	.0062	.77[b]	.0089
AL	-.142	.022	-.035	-.03[b]	-.0028	-.0478	-.0044	.00[b]	.0031	-.38[b]	.0027
D	-.128	-.114	.092	-.83[b]	.0149	.0034	-.0176	.23[b]	.0112	-.73[b]	.0070
DL	.158	.012	.292	1.12[b]	-.0196	.0326	.0158	.14[b]	-.0078	1.78[b]	.000[a]
E	.051	.002	-.055	.29[b]	.0003	.0111	-.0360	1.92[b]	.0406	1.76[b]	.0319

Table 49 (Continued)

	YLD	MOIST	KWT	SPGRAV	ER	KH	PROT	LYS	LP	HIST	HP	PYLD
A PYLD	.259	1.7	118.3	-.243	-15.42	-2.50	11.01	.312	-2.09	.175	-1.83	3120
AL	.177	-18.8	-20.9	-.174	2.53	20.88	1.04	-.114	-2.27	-.124	-1.79	1722
D	.393	-34.4	-116.8	-.400	-4.71	7.44	10.49	-.069	-5.60	.027	-2.46	4151
DL	-.223	5.8	51.7	.216	-.94	-15.46	-7.76	.270	7.04	.031	2.70	0[a]
E	.514	-19.6	62.1	.212	-1.07	4.68	14.34	.324	-3.35	.205	-2.11	5463
A LYLD	10.71	-.993	3.49	-.0201	-.686	-1.397	.300	.0234	.118	5.41[b]	-.0463	119.6
AL	6.74	-.588	-1.01	-.0108	.111	.637	.032	-.0039	-.075	-16.92[b]	-.0546	63.6
D	14.26	-1.515	-6.06	-.0340	.079	-.182	.307	.0066	-.059	5.31[b]	-.0155	114.3
DL	-6.60	-.122	6.83	.0274	-.316	.246	-.198	.0152	.264	.14[b]	.0350	-61.3
E	22.44	-.869	2.72	.0086	-.037	-.043	.284	.0407	.328	20.47[b]	.1462	213.2
A OPAC	4.73	-1.322	17.75	-.0651	.350	-7.37	-.516	.0271	.628	-.0075	.1025	8.33
AL	.16	-.368	-1.80	-.0182	-.062	.80	.100	.0223	.182	.0104	.0738	21.73
D	-1.32	-1.738	-4.09	-.0473	.648	-4.04	-.716	.0540	.928	.0177	.3482	-54.52
DL	2.76	1.606	5.36	.0104	.306	2.46	.670	-.0454	-.443	-.0170	-.4096	60.94
E	-2.26	-.614	-.05	-.0040	.072	-1.32	.334	.0357	.260	.0109	.0239	-1.15
A TWT	-.354	.607	-.579	.0194	-.1132	2.01	.128	-.0070	-.157	-2.09	-.0706	10.71
AL	-1.351	-.141	-.231	.0025	-.0136	-.24	.026	-.0011	-.017	-.21	-.0059	-9.40
D	.394	.235	.562	.0191	-.1943	.19	.113	-.0078	-.147	.76	-.0248	16.14
DL	1.920	.193	.098	.0088	.1192	.35	-.110	-.0008	.072	-.22	.0336	1.63
E	1.081	.097	.113	.0031	-.0708	.30	-.052	-.0024	-.012	-1.14	.0021	6.02
A KQUAL	-.731	-.190	-1.498	-.0010	.0221	-.251	.0122	.0026	.0251	1.48[b]	.0141	-5.51
AL	.132	.049	.082	.0014	.0028	.124	.0113	.0004	-.0025	-.17[b]	-.0058	.93
D	.077	.049	-.089	.0007	-.0105	.017	-.0455	-.0014	.0059	-1.28[b]	-.0006	-1.83
DL	-.904	-.098	-.360	-.0042	-.0120	-.147	.0318	-.0006	-.0168	.34[b]	-.0068	-6.14
E	-.068	-.004	-.092	.0004	.0076	.046	-.0014	.0008	.0081	.08	.0017	-.84
A KFRACT	-.392	-.1123	.413	.08[b]	.0857	-.088	-.0290	.0000	.0168	.61[b]	.0156	-5.11
AL	.361	.0438	-.118	-2.02[b]	-.0192	-.092	-.0129	.0000	.0061	-.13[b]	.0048	2.07
D	-.187	.0183	-.282	-1.13[b]	.0216	-.100	-.0301	.0007	.0220	-.77[b]	.0035	-3.98
DL	.012	-.2116	.873	1.94[b]	.0050	-.337	-.0276	-.0012	-.0036	-.02[b]	-.0014	-.74
E	-.006	-.0040	-.039	-.48[b]	.0329	.044	.0232	.0013	.0046	.24[b]	-.0037	1.12

Table 49 (Continued)

		LYLD	OPAC	TWT	KQUAL	KFRACT
A	LYLD	5.70				
AL		2.47				
D		6.04				
DL		.00[a]				
E		11.18				
A	OPAC	3.74	31.40			
AL		1.66	.00[a]			
D		3.37	7.45			
DL		-2.55	28.28			
E		1.64	26.68			
A	TWT	-.790	-6.60	2.225		
AL		-.477	.04	.000[a]		
D		-.093	-1.23	1.435		
DL		.483	-.65	.462		
E		.120	-1.77	.695		
A	KQUAL	-.0953	-.131	-.189	.0850	
AL		.0646	.200	.017	.0371	
D		-.0242	-.244	-.097	.0517	
DL		-.3610	.066	-.070	.000[a]	
E		.0107	.094	-.049	.1455	
A	KFRACT	-.1123	.433	-.152	.0071	.0472
AL		.1103	-.097	.037	.0003	.0078
D		-.0948	.512	-.077	.0201	.0162
DL		.0434	.066	-.093	-.0546	.000[a]
E		.0855	.089	-.064	.0219	.1613

Table 50. Estimates of phenotypic variances and covariances (S_0 plant basis) used in calculating selection indices, with variances on diagonal

	KH	PROT	LYS	LP	HIST	OPAC
KH	23.45					
PROT	1.982	.947				
LYS	.0464	.0339	.002006			
LP	-.396	-.0506	.00668	.103		
HIST	.0698	.0265	.001202	.00122	.001100	
OPAC	-56.03	.513	.1334	1.415	-.00897	380.6